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BOTANICAL SCIENCES

EDMUND W. SINNOTT, CONSULTING EDITOR

BOTANY

A TEXTBOOK FOR COLLEGES

T.B-47

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FRONTISPIECE. COLORATION IN PLANTS

1. Cherry leaf.
2. Leaf of yellow coleus.
3. Leaf of *Achyranthes*.
4. *Petunia* flower.
5. Flower of pot marigold (*Calendula*).
6. Flower of *Dianthus* (pink).
7. Enlarged view of cell of a moss leaf showing chloroplasts.
8. Enlarged view of cell of rose fruit showing chromoplasts.
9. Leaf-hair cell of velvet plant (*Gynura aurantiaca*).
10. Cherry.
11. Plum.
12. Yellow tomato.
13. Cucumber.
- 14-16. Alcoholic extracts of leaves to which benzol has been added, shaken, and allowed to settle.

The upper layer in each case is the benzol layer containing the green pigments, chlorophyll *a* and chlorophyll *b*; the lower layer is the alcohol layer containing in each case yellow carotenoid pigments and, in addition, in 15, anthocyanin. The yellow pigments in 15 are masked by the red anthocyanin. Green leaves were used in 14, red leaves in 15, and yellow leaves in 16.

17. A water extract of red leaves of *Achyranthes* containing anthocyanin.

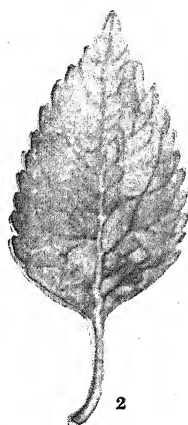
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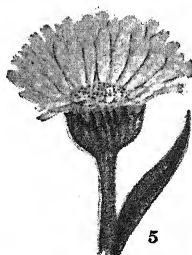
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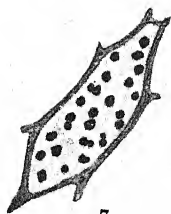
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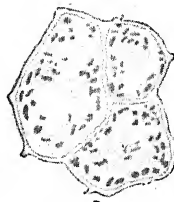
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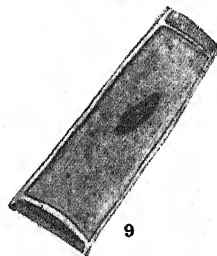
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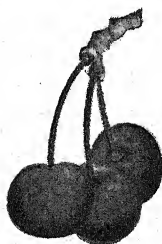
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COLORATION IN PLANTS
(Painting by Elsie M. McDougle.)
(For detailed explanation see reverse side of this page.)

BOTANY

A TEXTBOOK FOR COLLEGES

BY

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SECOND EDITION
THIRD IMPRESSION



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PREFACE TO THE SECOND EDITION

A revised edition of this text is necessitated by the many discoveries in the science of botany since the first edition appeared. Particularly is this true of the physiological aspects of the subject, although there is hardly a branch of botany in which substantial advances have not been made. Such subjects as antibiotics, vitamins, hormones and other growth substances, in their relation to plants, have come into such prominence in recent years as to make at least an elementary treatment of them an indispensable part of a general textbook of botany. For this reason, a brief consideration of these subjects as well as others has been included in the present revision. Some of the more recent research on such subjects as photosynthesis, respiration, fermentation, enzymes in general, and the use of "tagged" elements, while too complex for detailed treatment in a work of this kind, has at least been introduced.

The authors have also taken advantage of the opportunity to make corrections and changes suggested by their colleagues who have read sections of the text critically. Chapters 2, 3, 10, 12, 13, 16, and 19, and the first part of Chap. 11 have been entirely rewritten, and substantial changes have been made in most of the other chapters. A newer system of classification of the plant kingdom has been adopted in Part II of the book. This necessitated many changes in Chaps. 13 to 18. In Chap. 14, on the Algae, short sections on diatoms and on the Charales and a separate section on meiosis have been added at the request of several colleagues. The order of treatment of the different groups in Chap. 15 (originally entitled Fungi) has been changed, and sections have been added on viruses and actinomycetes. In addition, a general section on the economic importance of fungi has been included. On the other hand, the section on Myxomycetes has been shortened. The addition of new sections and reduction in others has been made so as to keep the size of the book approximately within the original limits.

A number of new figures have been added, and improvements have been made in more than 120 of the original figures. The use of borrowed figures has again been kept to a minimum.

The authors wish to take this opportunity to acknowledge the assistance given them in one way or another by many of their colleagues. They are particularly indebted to Dr. D. A. Kribs for the excellent photomicrographs he made especially for the revision; to Drs. G. W. Martin, H. M. Fitz-

patrick, J. W. Sinden, C. C. Wernham, W. R. Mills, and C. L. Fergus for reading and criticizing the section on fungi; to Dr. R. W. Stone for his suggestions concerning the section on bacteria; to Dr. C. O. Jensen for reading and criticizing the chapter on the catabolic phase of metabolism; to Dr. R. A. Dutcher for suggestions concerning the section on vitamins and hormones; to Drs. P. J. Kramer and F. G. Merkle for suggestions and criticisms on the discussion of absorption of water and minerals; to Drs. J. P. Kelly and Julia M. Haber for suggestions pertaining to the sections on flowers, fruits, and families of flowering plants; to Dr. H. A. Wahl for criticism of many sections of the book; to Drs. W. M. Atwood, A. R. Bechtel, E. F. Castetter, M. W. Eddy, E. J. Kraus, L. C. Petry, G. M. Smith, P. D. Strausbaugh, and W. R. Taylor for suggestions concerning one or another part of the book; to Mr. Homer I. Grove for assisting in photography and in many other ways; to Mr. and Mrs. Ross B. Lehman and Dr. Helen D. Hill for assistance with the manuscript; and to all those users of the text who have made suggestions of one kind or another.

THE AUTHORS

STATE COLLEGE, PA.
December, 1949

PREFACE TO THE FIRST EDITION

The contents of this book comprise the subject matter of a two-semester college course in general botany, in which Part I is usually given during the first semester and Part II during the second. The two parts, however, are relatively independent and could be given in the reverse order. In mimeographed form, this book has been used for several years by the authors and by others in classes consisting of students in agriculture, the liberal arts, and the sciences. Though now published for the first time, it has already gone through several revisions, prompted by the experience of the authors and others in using it as a text and by changing emphasis in the teaching of botany.

The sequence of subjects is the one that has proved to be most suitable for classes beginning in autumn. In determining this sequence, the authors have taken into consideration not only the logical advantage of passing from the relatively simple to the more complex, but also the expediency of introducing a subject when living materials are available for its study. None the less, the separate chapters have been written in such a way as to make it possible to adopt other sequences. Perhaps the most prominent departure from the sequence of other textbooks is the consideration of coloration in plants at the beginning. This has been done in recognition of the fact that color is one of the most conspicuous features of plants. It has been observed by everyone and immediately arouses interest. Furthermore, the display of colors in natural vegetation is most pronounced soon after classes begin in the autumn semester. A consideration of the cell, and then of the leaf and its physiology, logically follows. The root has been taken up before the stem because it is relatively a simpler structure than the latter. Cell division is discussed in the chapter on growth, not only because of its importance in growth but also because the student has acquired the necessary technique in the use of the microscope by the time the subject is treated. Throughout Part I, the physiology of an organ is considered in connection with its structure and morphology. Special emphasis has been given to physiology in general, but not at the expense of other phases of the general subject. Growth and metabolism have been particularly emphasized in the belief that these subjects deserve much more attention than they ordinarily receive in elementary courses. Part II is devoted entirely to a consideration of the different groups of plants. An attempt

has been made in this part of the book to give an adequate and balanced survey of the plant kingdom without undue emphasis on any one group of plants. The discussions have been made to conform in general to the newer discoveries that have become established.

The arrangement of the subject matter in each chapter is such that, where time does not permit the consideration of the entire chapter in the classroom, such parts as are most likely to be omitted are grouped near the end of the treatment or are printed in smaller type. This has been done in such a way as not to destroy the continuity.

A special effort has been made throughout the book to get away from the rapidly growing tendency of so simplifying the treatment of different subjects as to leave little of permanent value in the text. The authors are of the opinion that even a difficult matter, if adequately elucidated, can be understood by a beginner and should be included if sufficiently important to a general understanding of the subject. Furthermore, technical terms that have become thoroughly established and that contribute to scientific accuracy have not been avoided. In general, it is hoped that the book will be of sufficient value to the student to be retained by him for future reference when he has completed his elementary studies, especially if he does not specialize in botany.

The illustrations used throughout the text are, with few exceptions, new and original. Unusual care has been exercised in providing adequate and accurate illustrations. Microscopic views of plant tissues are mostly either photomicrographs or camera lucida drawings of actual structures. Gross structures are shown by photographs or drawings of the original material or by diagrams.

The authors are greatly indebted to the various persons who have assisted in the preparation of the illustrations or who have furnished photographs. Acknowledgment has been made individually in connection with each figure contributed. In addition, the authors wish to express their appreciation particularly to the following persons who have each made a considerable number of drawings: Mrs. Elsie Montague McDougale, Mrs. Edna Stamy Fox, Dr. Helen Deuss Hill, Miss Florence Brown, Mr. Ernest Geiswite, and Mr. Christian Hildebrandt. They are likewise indebted to the following persons for borrowed figures: to Dr. A. J. Eames and Dr. L. H. McDaniels for Figs. 29, 65, and 76, to Dr. J. E. Weaver for Fig. 41, to Dr. Gilbert M. Smith for Figs. 134, 135, 141, and 143, and to Dr. Charles J. Chamberlain for Fig. 286. The authors are especially indebted to Dr. Helen Deuss Hill for her untiring assistance in the preparation of the manuscript and in the arrangement and mounting of the figures as well as for her valuable criticism and to Miss Florence Brown for her criticisms and constant help in the preparation of the

manuscript. Their appreciation is likewise extended to Dr. F. D. Kern, Dr. J. P. Kelly, J. W. Sinden, H. A. Wahl and other members of the Botany Department of the Pennsylvania State College and to other persons who have read and criticized sections of the manuscript and assisted in one way or another.

THE AUTHORS

THE PENNSYLVANIA STATE COLLEGE
April, 1936





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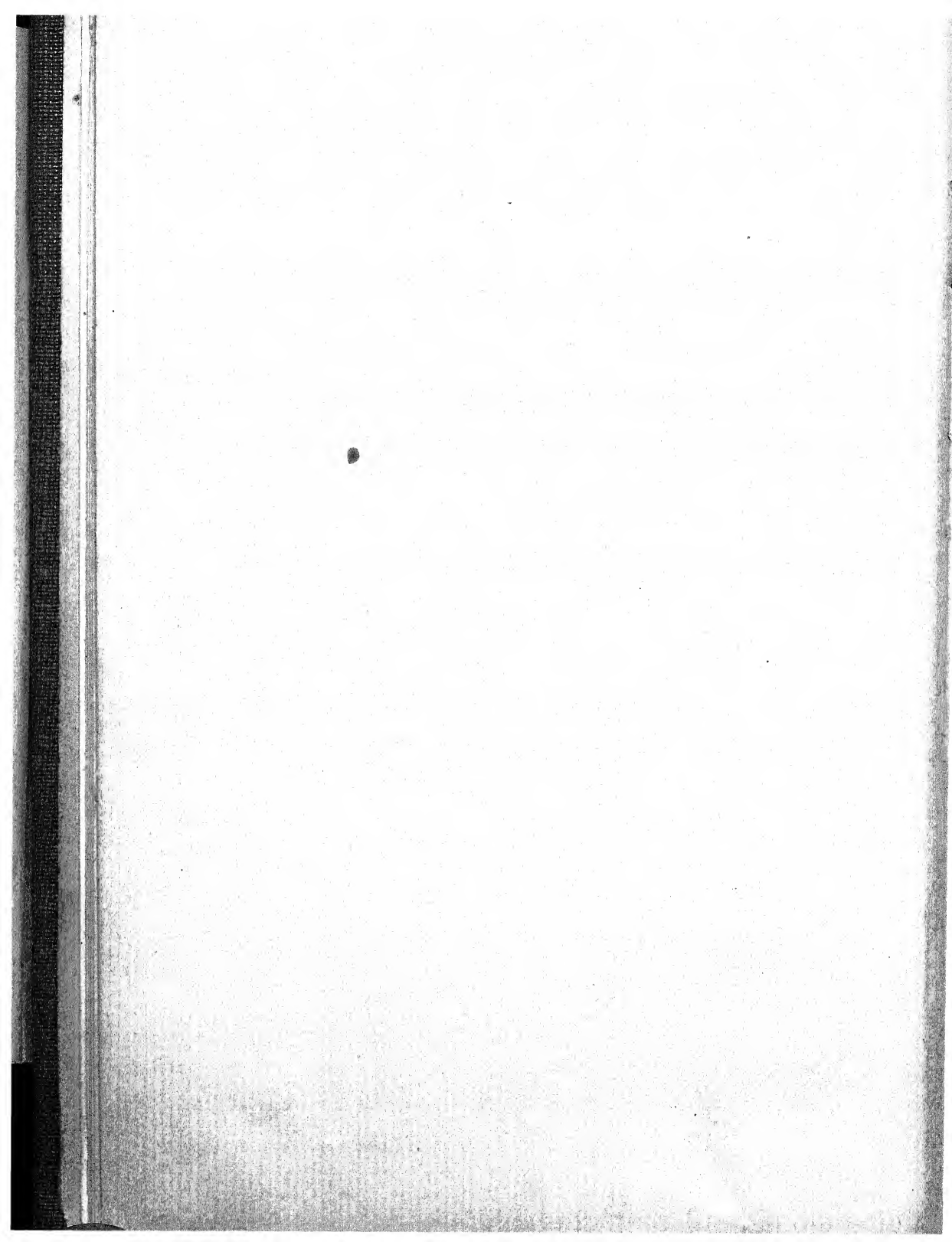
laceae (buttercup family), Cruciferae (mustard family), Solanaceae (potato or nightshade family), Scrophulariaceae (figwort family), Labiatae (mint family), Rosaceae (rose family), Leguminosae (pea or legume family), Umbelliferae (carrot family), Compositae (sunflower family), the "Amentiferae," Salicaceae (willow family)—Families of monocotyledons: Liliaceae (lily family), Orchidaceae (orchid family), Gramineae (grass family), Typhaceae (cat-tail family).

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Part I

STRUCTURE AND PHYSIOLOGY OF SEED PLANTS



CHAPTER 1

INTRODUCTION

Importance of Botany. Botany is that branch of science which deals with the study of plants. Beginning students, and particularly those who are specializing in other departments of learning, are often at a loss to understand why they should be required to devote any time to the study of plants. A little thought on the matter, however, will show that plants occupy a very prominent position in our everyday lives. So prominent is this position that it can truthfully be said that no man is educated in the broad sense who knows nothing about plants. Whether we enjoy studying plants or not, we must depend upon them for practically all our food, clothing, and shelter. Moreover, it is the green plants that keep the air we breathe supplied with oxygen, the absence of which would probably mean the extinction of all life on earth. Not only do they supply us with all our primary biological needs but they also cause many of the most serious diseases of man. At the same time, they provide many of the medicines used to cure disease. Furthermore, it is by working directly with plants or with plant products that a majority of the world's workers earn a living.

These facts have existed from the beginning of man and have played a decisive role in his history and civilization. Down through the ages we find plants ministering to the needs of man and determining his progress. Wars were caused on account of plants and won by means of plants. New lands were discovered in the search for plants. We need only mention the search for a new route to the land where spices and other useful plants grew, which led Columbus to the discovery of America, or the influence of cotton on the Civil War to show the controlling influence of plants in our own country's history. The thoughtful student will be able to adduce many similar examples (see also page 281).

The study of plants by some of the world's most accomplished scientists not only has added immeasurably to man's general enlightenment and understanding of the universe but has resulted in vast improvements in the production of farm crops, in manufacturing processes, in medicine, and in all things that assuage the rigor and augment the comforts of life and raise man's standard of living.

Much could also be said of the aesthetic value of plants and the part it has played in the production of such masterpieces as Bryant's "Thanatop-

sis" or his "Forest Hymn," Emerson's "Rhodora," Moore's "Last Rose of Summer," or Joyce Kilmer's "Trees." Indeed, plants have been the incentive for the production of some of the most beautiful works of art, literature, and music. Furthermore, the study of plants has proved to be a most pleasing and gratifying avocation for lawyers, bankers, physicians, and other professional men.

It is obvious, in consideration of these facts, that a general knowledge of objects which constitute so large a part of our environment and play so prominent a part in our lives is essential to a broad education. From the purely utilitarian point of view, a knowledge of the fundamentals of botany is absolutely indispensable to the student of agriculture or biology. He should very early grasp this fact so that he may better master the basic facts that form the foundation on which his later, more specialized agricultural or biological structure is built.

Branches of Botany. Botany is one of the main divisions of biology, the science of life. Other branches of biology include zoology, biochemistry, biophysics, psychology, and the medical sciences. The element common to all of these fields of learning is the fact that they deal with living organisms. This emphasizes the fact that plants are living organisms and as such have many things in common with other forms of life.

For convenience of study the subject of botany has been divided into several important branches. Among these are taxonomy, morphology, physiology, pathology, ecology, paleobotany, and plant genetics. **Taxonomy**, or systematic botany, deals with the classification of plants. **Morphology** considers the form and structure of plants, together with the relationships of the parts of plants to each other, and comprises a study of anatomy, cytology (study of the cell), and embryology. **Physiology** is concerned with the life processes of plants and the functions of the different organs and tissues. **Pathology** deals with diseases of plants; **ecology**, with the relations of plants to their surroundings; **paleobotany**, or fossil botany, with the plants of past geological periods; and **plant genetics**, with the study of heredity in plants.

Other branches of the subject are concerned with an intensive study of separate groups of plants. Thus **bacteriology** is confined to the study of bacteria, **mycology** to the study of fungi, **algology** to the study of the algae, and **bryology** to the study of mosses.

In addition to these definite branches of botany, many of the agricultural and other sciences either have had their origin in botany or may be considered as resting on a foundation of botany. Among these may be mentioned horticulture, forestry, landscape gardening, floriculture, plant breeding, and to some extent agronomy and pharmacy.

Different Kinds of Plants. An excursion into the woods or fields during

the summer or autumn reveals a wide diversity of form and structure in the plants encountered. Some are tall trees; others are low-growing herbs or shrubs; some have beautiful flowers and produce seed, while others, like the ferns, produce no flowers at all but reproduce by means of tiny structures called spores; some live on land, others in water; some are giants, while others are so small as to be seen only with a microscope. These wide differences led botanists years ago to attempt to arrange plants into different groups for the convenience of study and discussion. Many different systems of classification have been used but the one most generally accepted is based upon fundamental similarities or relationships and is called the natural system. According to this system, the entire plant kingdom is usually subdivided into several large main divisions. Each of these is then subdivided into appropriate groups. A discussion of the systems of classification may be found in Chap. 13. It will suffice here to call attention merely to some of the different kinds of plants that make up the plant kingdom.

Among the plants lowest in development, with the least structural differentiation, are the bacteria, the fungi, and the algae. These plants have no roots, stems, or leaves. A plant body of this type is called a **thallus**. The simplest of these plants are the bacteria, most of which are unicellular, *i.e.*, the entire plant consists of but a single cell. Hence, the individual plants are visible only under the high magnification of a microscope. They are commonly called microbes. These organisms are universally present in the soil, in air, in water, on decaying animal and vegetable matter, or in other living organisms where they sometimes cause serious diseases. They are of vast importance to man in many ways. Pneumonia, tuberculosis, influenza, various infections, and many other diseases of human beings are caused by bacteria. On the other hand, many of the bacteria are extremely beneficial to man. This is especially true of soil bacteria.

Molds, mildews, yeasts, smuts, rusts, mushrooms, and toadstools (Fig. 1, B) are examples of fungi. Like the bacteria, the fungi all lack the green chlorophyll pigments essential for independent existence, and hence they must get their food from other living organisms or from dead or decaying organic matter. Some of the fungi, like the rusts and smuts, cause serious diseases of crop plants. Others cause diseases of human beings and of other animals. Many, however, are of great benefit to man. Thus, mushrooms are used as food; yeasts are highly important in the baking, brewing, and wine-making industries; and many of the soil fungi are important in crop production. Penicillin and other antibiotics obtained from fungi in recent years have become extremely important in medicine.

The algae, examples of which are the common pond scums and seaweeds,

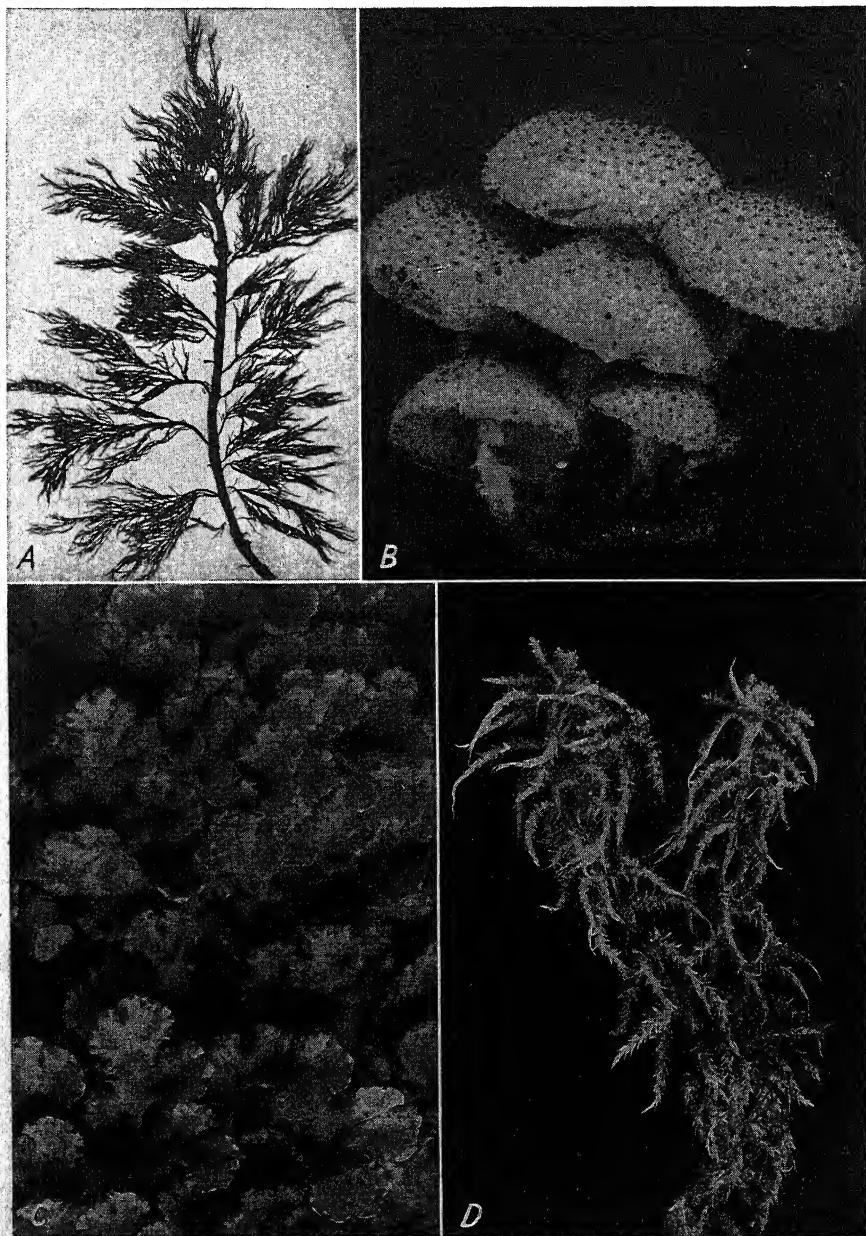


FIG. 1. Different kinds of plants. A, the red alga (*Polysiphonia*), a seaweed; B, *Pholiota squarrosoides*, a fungus; C, *Marchantia*, one of the liverworts; D, *Sphagnum*, one of the mosses.

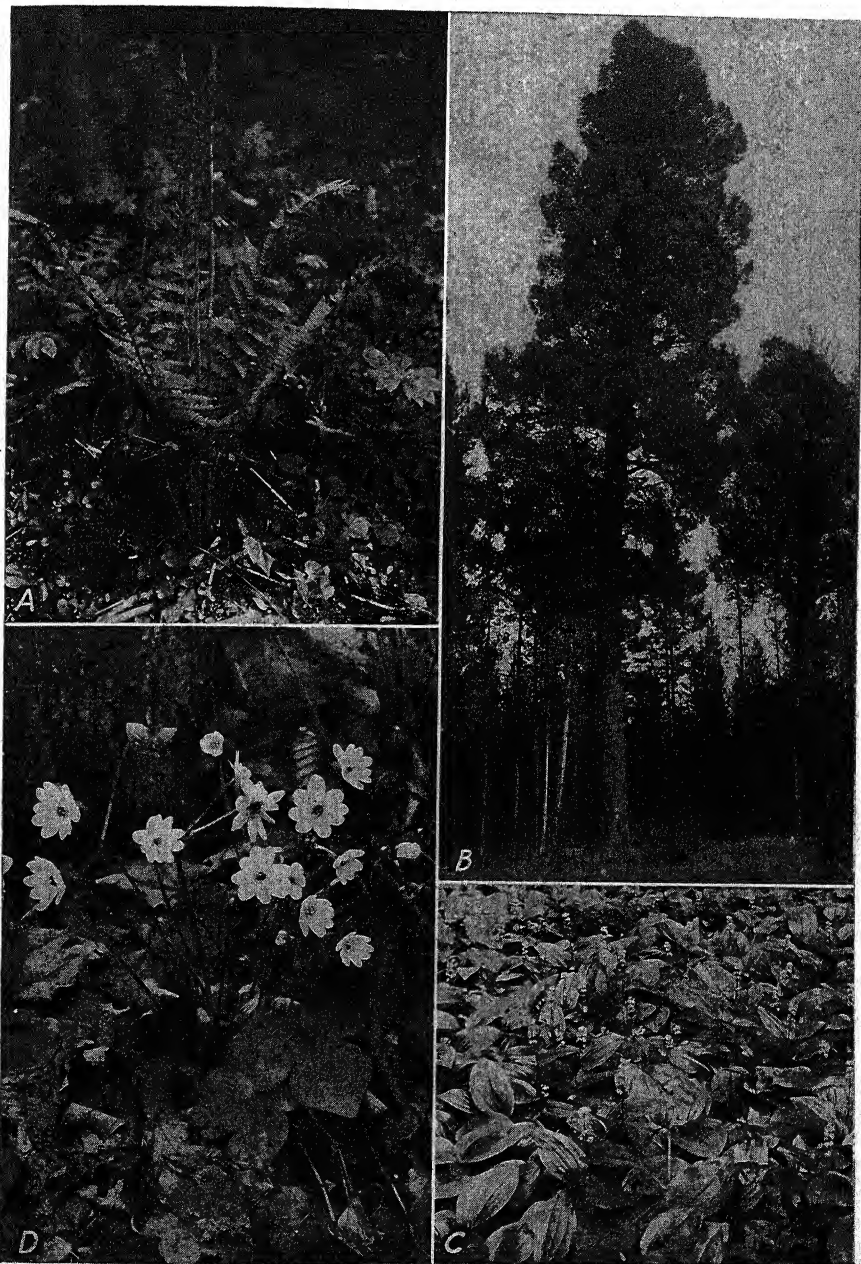


FIG. 2. Different kinds of plants. A, *Osmunda cinnamomea*, a common fern of northern woods; B-D, seed plants; B, *Pseudotsuga taxifolia* (Douglas fir), a western member of the gymnosperms; C, false lily of the valley (*Maianthemum canadense*), a monocotyledonous angiosperm; D, *Hepatica acutiloba*, a common spring flower, one of the dicotyledonous angiosperms. (B, photograph by A. S. Rhoads.)

usually grow submerged in water or in moist situations. Some are found in soil, and others grow on the bark of trees. They are of various colors, green, brown, red, and blue-green, but most of them contain the green chlorophyll pigments and hence are independent plants. Many of the algae are either unicellular or consist of a colony of cells. Most of them are relatively simple in structure, although some of the larger seaweeds show considerable tissue differentiation (Fig. 1, *A*). Algae are of economic importance as the food basis for all aquatic animal life. They also make up an important part of the soil flora essential in soil productivity.

The mosses and their relatives, the liverworts, make up a group of plants commonly found growing in moist places throughout the world. These plants also lack roots, stems, and leaves, in the sense that we think of these structures in higher plants (Fig. 1, *C*, *D*). The liverworts and mosses differ from algae not so much in size or appearance as in their reproductive features. Whereas the reproductive organs of algae are generally single-celled structures, those of the liverworts and mosses are multicellular. Although liverworts and especially the mosses add considerable beauty and interest to the wild landscapes of the world, compared with the algae and fungi, they are of only slight economic importance.

The common ferns and associated groups, the horsetails or scouring rushes, together with the Lycopodiums and Selaginellas, or club mosses, differ from the algae, fungi, liverworts, and mosses in that they have more highly differentiated plant bodies (Fig. 2, *A*). They have true roots, stems, and leaves, and a well-defined vascular, or conducting, system. They differ from the higher plants in that they do not produce flowers, fruits, or seeds. Some of these plants, especially the ferns, are ornamental plants and as such have some economic value. In general, however, these plants are economically of minor importance.

The plants with the highest development and greatest differentiation are the seed plants. They have true roots, stems, and leaves and a highly developed vascular, or conducting, system. The most important feature about them, however, is the fact that they produce seeds. It is to this group that all crop plants belong, as well as all the common trees, shrubs and flowering plants with which everyone is familiar. Any plant that forms true seeds belongs to this group.

Since practically all of the first half of this textbook deals with the seed plants, it may be well to consider briefly the two principal groups of seed plants. They are the **gymnosperms** and the **angiosperms**. The gymnosperms are characterized by producing their seeds exposed, *i.e.*, not enclosed in a fruit. The term "gymnosperm" means "naked seed." The gymnosperms are represented in the north temperate regions by the pines, spruces, hemlocks, cedars, and other evergreens (Fig. 2, *B*). Many of

them bear their seeds in cones, and none of them has conspicuous flowers. The angiosperms, on the other hand, have well-developed flowers and produce their seeds in an enclosed structure which is called the fruit. The term "angiosperm" means "enclosed or hidden seed." The members of this group are very numerous and embrace all the well-known flowering plants. The angiosperms are further subdivided into two coordinate groups, the **monocotyledons** and the **dicotyledons**. The monocotyledons (Fig. 2, *C*) are represented by the grass-like plants, such as corn, wheat, oats, and other cereals, and by such plants as the lilies, orchids, bamboo, and banana. To the dicotyledons (Fig. 2, *D*) belong all the broad-leaved forest trees and many ornamental and crop plants, such as clover, beans, peas, buckwheat, and geranium. The essential differences between these two groups can best be considered later in the text.

CHAPTER 2

COLORATION IN PLANTS. PLANT PIGMENTS

Of the common external characteristics of plants the most impressive and distinctive is probably color. Color is not only a conspicuous feature of vegetation but some of the pigments responsible for color are closely tied up with the physiological activities of the plant itself. Hence, a knowledge of plant pigments is essential to an understanding of how plants live and grow.

While it is possible to find in the plant kingdom as a whole all shades and combinations of the colors of the spectrum, there is in general a predominance of the primary colors: green, yellow, red, and blue. These colors are imparted to the plant by definite chemical compounds, or pigments, each of which has its own characteristic color. The particular color which a plant organ assumes is usually caused by the predominance of one or another of these pigments in a combination of several of them. When plant parts appear white, it is because of the absence of pigments. Sunlight falling on such parts is not so selectively absorbed as it is in colored parts but is transmitted or reflected practically as received, and hence such parts appear white or colorless. The opaqueness of this white is intensified by the refractive powers of cell walls and often by the presence of air spaces in the tissues.

The Chlorophylls. The green color so uniformly present in plants is caused by the presence of two closely related pigments which have been designated as **chlorophyll a** and **chlorophyll b**. These two pigments are commonly referred to simply as chlorophyll. They occur in practically all seed plants, ferns, mosses, and algae. They may develop in roots, stems, leaves, and fruits, provided that these organs are aboveground and exposed to light (frontispiece, 1, 13). They are not normally present in internal tissues where light does not penetrate, such as the wood of a tree or the flesh of an apple, nor are they usually found in underground structures like roots and tubers. Though apparently absent in red or yellow leaves, when the other coloring matters are extracted from such leaves, the chlorophylls may be found to be present even there, having been obscured by other pigments. Thus red *Coleus* or red *Achyranthes* leaves when boiled in water become green after the red has thus been extracted. The chlorophyll pigments are actually absent, however, in such lower plants as the

bacteria, mushrooms, toadstools, and other fungi, and in such flowering plants as the Indian pipe and beechdrops. The absence of the chlorophylls has a profound effect on the method by which plants obtain their carbohydrate food. Green plants, by means of their chlorophyll, are able to manufacture their own foods, while plants lacking chlorophyll are dependent for their food on other plants or animals.

Condition within the Cell. Within the cells in which they are found, the chlorophyll pigments are contained in tiny rounded or elliptic bodies called **chloroplasts**. Chloroplasts are merely plastids containing chlorophyll pigments (frontispiece, 7). A plastid is a denser bit of that living substance known as protoplasm and is to be regarded as the container of the chlorophyll pigments. When the pigments are extracted, the plastid still remains. Plastids that contain no coloring matter are called **leucoplasts**. When a plant grows in the dark and is more or less colorless, leucoplasts may be present in the cells. If such a plant is brought out into light, chlorophyll pigments may be formed in these plastids, whereupon they become chloroplasts. The chloroplasts themselves are made up of rather complex organic substances, including proteins and other colloidal materials. There is some evidence that the chlorophyll pigments may be tied up chemically with the proteins of the chloroplasts. In any case, they are held in colloidal condition. Associated with the two chlorophylls there are also in the chloroplast two kinds of yellow pigments, *viz.*, carotenes and xanthophylls, or carotenols, to be discussed later. Thus a chloroplast contains four kinds of pigments, two that are green and two that are yellow.

Extraction and Properties. The chlorophyll pigments are not soluble in water even under prolonged boiling but may be readily extracted from green tissues by the use of ethyl, or grain alcohol, methyl, or wood alcohol, acetone, ether, chloroform, or benzene. When these solvents are used, other pigments are extracted simultaneously. Thus an alcoholic extract of green leaves is a solution consisting of several pigments. When an equal quantity of benzene is added to such a solution and the mixture is gently inverted several times, it separates into two layers, an upper green layer and a lower yellow layer (frontispiece, 14). The upper layer contains the two green pigments dissolved in benzene, *viz.*, chlorophyll a, $C_{55}H_{72}O_5N_4Mg$, and chlorophyll b, $C_{55}H_{70}O_5N_4Mg$, while the lower alcoholic layer is a solution of yellow carotenoid pigments. When red leaves are used for extraction, the lower alcoholic layer appears pink to red (frontispiece, 15) owing to a red pigment present in red leaves, while with yellow leaves the yellow of the lower layer is intensified (frontispiece, 16) because of the relatively higher percentage of carotenoid pigments present in such leaves.

Alcoholic extracts of green leaves are fluorescent, *i.e.*, they appear green by transmitted light and brownish red by reflected light. A pure alcoholic

solution of chlorophyll a is blue-green by transmitted light and blood-red by reflected light. An alcoholic solution of chlorophyll b is yellow-green by transmitted light and brownish red by reflected light. If the alcoholic extract of green leaves is allowed to stand in bright sunlight for an hour or two, the solution becomes a dirty brown color, indicating the destruction of the chlorophyll pigments by sunlight. A similar destruction probably occurs in living leaves, but since the chlorophylls in this case are bound up with the colloids of the plastid, the destruction is not nearly so rapid, and in addition new chlorophyll pigments are constantly being manufactured. Hence, there is no change in color of green tissues in light so long as they remain in a healthy and vigorous condition.

The chloroplasts of all higher plants contain both chlorophyll a and chlorophyll b, but in some of the lower plants (diatoms and some of the red, brown, and blue-green algae) chlorophyll b may be absent altogether or be present in very minute quantities. Two additional chlorophylls, chlorophyll c and chlorophyll d, have been reported to be present in some of these plants. Of the total green pigment present in leaves, usually about three fourths is chlorophyll a and one fourth chlorophyll b. Apparently the proportion of chlorophyll b is larger in plants grown in the shade than in plants exposed to direct sunlight.

Conditions Necessary for Chlorophyll Formation. Exactly how plants manufacture the chlorophyll pigments has not yet been determined, but it is well known that certain conditions and substances are necessary for their formation. There must be light of proper intensity. A medium light intensity is most favorable. Plants grown in total darkness do not become green. This is well illustrated by potatoes growing in cellars or by grass growing under boards. Frequently, when plants that are already green are placed in the dark, they lose their green color, as occurs in the blanching of celery. With most plants, however, a long period of darkness is required for complete blanching. A favorable temperature is also necessary for chlorophyll formation, medium temperatures being best. There is little, if any, greening at temperatures lower than 2 to 4°C., or higher than 38 to 40°C. Most rapid formation occurs at about 20 to 30°C. In addition there must be an available supply of oxygen and of salts containing iron, nitrogen, magnesium, and possibly other mineral elements. Nitrogen and magnesium occur in the molecules of both chlorophylls. A trace of iron salts is necessary even though iron is not a part of the molecules of these pigments. Finally, plants cannot synthesize chlorophyll pigments unless they have a supply of sugar, such as cane sugar or glucose. When any of these substances or conditions are deficient, plants tend to assume a white or yellow appearance, a condition which is called **chlorosis**. Chlorotic plants make poor growth and often die unless the condition is corrected.

Importance of Chlorophyll Pigments. The details of the function of chlorophyll pigments in the plant are taken up later in the text, but it may be stated here that they are necessary in the plant for the manufacture of carbohydrates such as grape sugar, fruit sugar, and starch, substances which form the basis of all foods for both plants and animals and which enter into the composition of all plant tissues. It is for this reason that the chlorophyll pigments are regarded among the most important chemical substances in nature.

The chlorophyll pigments are used to some extent in medicines and as a coloring for waxes, candles, resins, soaps, foods, and oils. A pound of fresh leaves yields about 0.5 to 1 g. of pure chlorophyll. While this seems a small amount, it has been estimated that in the United States alone more than 6 million tons of chlorophyll are produced yearly by corn and the small grain crops alone.

The Carotenoids. A number of yellow, orange, or sometimes red-colored pigments, collectively known as the **carotenoids**, are found in plants. More than 60 different kinds of these pigments have been isolated thus far. They may be divided into two principal classes, *viz.*, the **carotenes** and the **xanthophylls**, or **carotenols**. Often these two classes of pigments are found together in the same cell. As has been stated in a previous paragraph, they are both present with the chlorophylls in the chloroplasts, often giving to healthy green leaves a decidedly yellow tinge. They are not restricted to the chloroplasts, however, but are also found in the absence of the chlorophylls, in yellow to orange-colored plastids known as **chromoplasts** (frontispiece, 8). They are always found in plastids and never dissolved in the cell sap. Chromoplasts are found in many flowers, fruits, seeds, and roots as well as in leaves (frontispiece, 2, 5, 12). While the colors of the carotenoid pigments may range from yellow through orange to red, the commonest color is yellow.

When the chlorophylls are extracted from green leaves with alcohol, some of the carotenoid pigments are removed at the same time. As previously stated, they can be separated from the chlorophylls by adding benzene to the extract, in which case the carotenoid pigments remain in the lower alcoholic layer (frontispiece, 14, 16). Carotenoids are not readily decomposed by light or heat and hence, when associated with the chlorophylls, they become prominent after the leaf vitality begins to wane in the autumn. The carotenoids are also widespread in lower plants and in animal tissue such as the fat of many animals, egg yolk, and butterfat.

The Carotenes. Chemically the carotenes are hydrocarbons (compounds consisting of only carbon and hydrogen), most of which have the general formula $C_{40}H_{56}$. They are insoluble in water or aqueous alcohol but can be extracted readily with petroleum ether, ethyl ether, chloroform, or car-

bon disulfide. It is the occurrence of carotenes in the roots of the carrot that gives these roots their bright yellow color and from its presence in this plant originated the name of this class of pigments. The commonest one found in green plants is β -carotene. α -carotene and γ -carotene are also common in green and yellow leaves, in carrots, in pumpkins, and in other parts of plants. Another well-known carotene is **lycopene**, found in the fruits of the tomato, the pepper and other members of the nightshade family, in rose hips, apricots, citrus fruits, marigold flowers, orange blossoms, and in many other seed plants and even in some of the bacteria.

β -carotene and a few other carotenes are converted into fat-soluble vitamin A in the animal body. It is for this reason that carrots and leafy vegetables in general are important dietary sources of this vitamin.

The Xanthophylls; or Carotenols. **Xanthophylls** (meaning leaf yellow) were first isolated from leaves. Most of those who work with carotenoid pigments prefer to call them **carotenols**. They differ from the carotenes in that they all contain oxygen in addition to carbon and hydrogen and hence are not hydrocarbons. They also differ in solubility, being insoluble in petroleum ether and only slightly soluble in carbon disulfide, but readily soluble in ethyl alcohol. Like the carotenes they are insoluble in water but readily soluble in ethyl ether. The different kinds of xanthophylls differ in chemical constitution and properties, but many of them are alcohols. They are a much larger group than the carotenes. The most abundant xanthophyll in leaves is **luteol** (lutein), $C_{40}H_{54}(OH)_2$. It also occurs in many yellow flowers, such as those of the sunflower and the dandelion, and in egg yolks. **Zeaxanthol** (zeaxanthin), $C_{40}H_{54}(OH)_2$, is the chief yellow pigment of corn (maize). **Fucoxanthol** (fucoxanthin), $C_{40}H_{60}O_6$, is one of the principal pigments of the brown algae.

Possible Functions of Carotenoid Pigments. The functions of the carotenoid pigments in the plant are not known, except that some of them, as already mentioned, are involved in vitamin A production, which may be as important to plants as it is to animals. Their presence in flowers is thought to attract insects and thereby to secure cross-pollination. Their presence in fruits may render fruits more attractive and thus secure for them a wider distribution by animals. The universal association of carotenoid pigments with the chlorophylls has led many investigators to attempt to demonstrate a function for these pigments in carbohydrate manufacture. Attempts have also been made to associate them with the process of respiration in plants, but thus far no absolute proof of such functions has been demonstrated. The relation of the carotenoids to vitamin A renders these pigments of great importance to both plants and animals and has stimulated a vast amount of research on them in recent years.

The Anthocyanins. Most of the red, blue, and violet colors of plants ranging from the mosses through the seed plants are caused by a class of

chemical compounds known as **anthocyanins**. These pigments are not contained in plastids as are the chlorophylls and carotenoids but are found dissolved in the cell sap of the cell. They, therefore, usually appear uniformly distributed throughout the cell (frontispiece, 9). In some cases they occur as crystals. The red or purplish leaf hairs of the "velvet plant" (*Gynura aurantiaca*), the red roots of the common beet, the red lower surface of the leaves of wandering Jew and other plants, many red, blue, or violet flowers and fruits all owe their colors to anthocyanins (frontispiece, 4, 6, 10, 11). In leaves, the anthocyanins sometimes completely obscure the chlorophyll pigments, as in red cabbage or in *Achyranthes* (frontispiece, 3).

Extraction and Properties. Chemically the anthocyanins are glycosides, *i.e.*, compounds which, on being broken down into less complex components, yield, among other substances, a sugar. The nonsugar part of a glycoside is called an **aglycon**. The aglycons of the anthocyanins are called **anthocyanidins** and are rather complex organic compounds with a similar organic nucleus. The commonest sugar component is glucose, but several other sugars may be found. Some anthocyanins contain one molecule of sugar, and some contain two. There are many different kinds of anthocyanins in different species of plants. Two or more kinds are often present in the same species.

The anthocyanins are all soluble in water and can also be extracted with alcohol. They are not soluble in ether, chloroform, or benzene. The red color obtained when beets or red leaves are boiled in water (frontispiece, 17) is caused by anthocyanins.

Their color in the plant depends upon a number of factors among which may be mentioned the concentration of the anthocyanin, the simultaneous presence of several anthocyanins and other pigments, the ash content of the cell sap, the colloidal condition of the cell content, and the hydrogen ion concentration of the cell sap. Of these, the last has been most emphasized. When the cell sap is acid in reaction, the color is often red (frontispiece, 3) and when the cell sap is alkaline, it is usually blue (frontispiece, 4, 11). This can be demonstrated in the laboratory by placing blue flowers in a weak acid solution. After enough time has elapsed to permit penetration, they become red in color. Similarly, pink or red flowers will often turn blue in weak ammonia. The same thing may be demonstrated by extracting the pigments of blue flowers with water and adding acid to the extract. It immediately changes to a cherry red. Adding an alkali to the extract usually does not give a blue but a yellowish-green color because of the presence of yellow flavone pigments and other impurities.

Factors Affecting Anthocyanin Formation. In many species of plants the production of anthocyanins is an hereditary character, *i.e.*, such plants come true to color from seed. This fact is utilized by plant breeders. The

intensity of color, however, is often greatly influenced by environmental conditions and by internal factors. Purple-leaved types of lettuce, for example, fail to develop anthocyanin when deprived of blue-violet and ultraviolet radiation, and many highly colored flowers and leaves become much paler under these conditions or under weak light. Some plants do not develop anthocyanin in darkness, while others, like beets, do. Temperature, the internal food supply, the supply of inorganic substances, disease and injury, and perhaps other factors may affect the formation of these pigments. Often anthocyanin does not appear until late in the season as a result of ordinary ripening processes, as in apples and other fruits. The exact mechanism of the formation of anthocyanins in the plant is not known, but it is likely that sugars are involved in their synthesis, not only as the sugar component but also in the formation of the aglycons.

Possible Functions of Anthocyanin Pigments. The function of the anthocyanin pigments has been much in dispute. Where they occur in flowers, the colors have been thought to guide or attract insects or humming-birds and thus facilitate cross-pollination. By some it is thought that anthocyanins in some plants, as in the tender opening foliage of maples, act as a protective screen against intense sunlight and especially ultraviolet radiation, which may be injurious to living protoplasm. Another theory is that anthocyanins absorb certain of the sun's rays and transform them into heat, which raises the internal temperature of the parts in which the pigments occur and thus protects them against low temperatures. In favor of both of these ideas, it may be stated that plants growing in high altitudes, where it is cooler and where the intensity of the ultraviolet portion of sunlight may be greater, usually develop much more anthocyanin than do plants in lowland regions. However, in the present state of experimental evidence, it must be admitted that neither of these theories rests on a firm foundation. The same may be said of attempts to link the anthocyanins with various physiological processes such as respiration and food synthesis or to consider them as reserve food substances or waste products of metabolism. The varied distribution of these pigments, their presence in so many different organs of the plant, the different conditions under which they are formed, and other factors will always make it difficult to assign to them specific functions.

The Flavones. Another group of pigments fairly widespread in plants are the flavones. Their color is yellow and is often masked by other pigments. Water extracts of green leaves often have a yellowish tinge caused by these pigments. The flavones, like the anthocyanins, are water soluble and hence occur in the cell sap and not in plastids. Chemically, they are related to the anthocyanins. One of the most common of them is **quercetin**, $C_{15}H_{10}O_7$, which has been isolated from such plants as sumach, horse chestnut, tea, hops, onions, and the North American dyer's oak

(*Quercus tinctoria*). Many of the flavone pigments were formerly used as mordant dyes.

Autumn Coloration. A consideration of color in plants would not be complete without some reference to the brilliant display of color manifested each autumn, particularly in the leaves of trees and shrubs. Our knowledge of the underlying causes of autumn coloration is far from complete. Two types of factors are probably involved. On the one hand are the internal physiological conditions of the leaf itself, particularly those concerned with pigment development, and on the other the changing external conditions of the environment.

Primarily, autumn coloration is associated with the waning vitality of the leaf. As the growth season draws to a close, a special layer of cells known as the abscission layer is formed through the base of the leaf (Fig. 29). The cells behind this layer become corky and impervious to water, and the water-conducting vessels themselves often become clogged. The transport of materials to and from the leaf is thus seriously checked. This reduces the activities of the leaf and interferes with the development of chlorophyll. Since chlorophyll is being continually destroyed by sunlight, the leaves soon lose their green color when more chlorophyll cannot be made to replace this loss. This allows any other coloring matter that may be present to show up and also is conducive to the formation of other coloring substances, although probably these new ones do not originate from the decomposition of the chlorophyll, as formerly believed. Thus the principal foundation on which autumn coloration rests is the destruction of the chlorophyll, thereby allowing other pigments formerly masked to become prominent, and the formation of new coloring matters not previously present in the leaf.

As previously mentioned, the yellow carotenoid pigments are constantly associated with chlorophyll. Because of the greater stability of these pigments in sunlight, they persist in the leaves after the chlorophyll is destroyed. In the absence of other coloring matters, therefore, autumn leaves are yellow in color, and in some trees, like the ash, walnut, sycamore, poplar, and some birches, this is the predominating if not the only color shown. In others, the yellow, while always present, becomes masked by secondary coloring compounds that are formed. Yellow must be regarded as the most universally present, though perhaps not the most conspicuous, autumn color.

The red colors that appear in autumn vegetation are caused by pigments often not previously present in the leaf but formed after the vitality of the leaf begins to decline. The exact manner of their origin is not known. That light is influential is shown by the fact that leaves of such trees as maples and oaks, if kept covered or well shaded, do not become red but show only yellow. The disappearance of the chlorophyll tends to admit more

light to the leaf, which may affect the development of the red pigments. It is perhaps partly for this reason that the brightest colors are often found in vegetation when the autumn season is bright and sunny rather than dull and cloudy.

It is often found that leaves which develop the greatest intensity of red, like the maples, are rich in sugar.

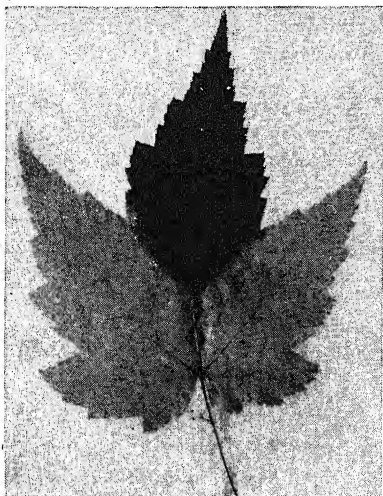


FIG. 3. Autumn maple leaf in which the central vein has been injured by insect or fungus attack. The dark portion above the injury was bright red, while the rest of the leaf was yellow.

The presence of sugar in a leaf is probably essential for anthocyanin formation. Furthermore, coloration is usually richest in seasons when there is an abrupt change from high summer temperatures to low autumn temperatures. Under such conditions the movement of sugars and other materials out of the leaf may be retarded and thus provide the conditions conducive to pigment formation. Further evidence of the possible influence of sugars and other substances of the leaf on the development of anthocyanin is furnished by leaves in which one or more of the veins have been cut or injured (Fig. 3). It is often found in such cases that the portion of the leaf formerly supplied by the cut vein turns a bright red, while the rest of the leaf may turn yellow in autumn. The cut or injury probably occurs while there is still considerable

sugar in the leaf; and since the sugar cannot be translocated from the severed section, it remains available for anthocyanin formation. The portion above the cut in such leaves usually remains green longer than the other portions of the leaf but finally turns red in leaves that make anthocyanin.

Frost may play a part in autumn coloration, but that it is not essential is indicated by the fact that leaves frequently turn red or yellow before the first frost occurs.

The discussion thus far has been concerned with the three predominating colors of autumn vegetation. The various shades, ranging from brilliant red to orange and golden yellow, usually result from combinations of these three colors. These brilliant colors usually last for only a comparatively short time. As the season advances and the nights become colder, the colors gradually fade, through internal disorganization of the pigments and other leaf compounds, and the leaf dies. Decomposition products accumulate, and the leaf assumes a brown color and falls to the ground.

CHAPTER 3

PLANT CELLS

INTRODUCTION

The plant body of a seed plant is made up of distinct parts, or organs, known as roots, stems, leaves, flowers, fruits, and seeds. These organs are composed of various kinds of tissues, such as storage, conducting, supporting, and protective tissues. Tissues in turn are made up of structural and physiological units called cells. The study of the cell is of great importance because it is the unit of structure, the seat of the vital physiological processes of the organism, and, in the case of the reproductive cells, the bearer of the hereditary material from one generation to another.

The history of the discovery of the cell and the development of the cell theory to the modern concept of the cell forms one of the most interesting chapters of biological literature. It is sufficient for the purpose of this discussion to state that the cell as a unit of structure was first seen by Robert Hooke, an Englishman, in 1665, and that the cell theory, which postulates that all plants and animals are composed of fundamental structural and physiological units, was formulated by Schleiden and Schwann, two Germans, in 1838-1839. The name cell was given to the fundamental structural unit of plants by Robert Hooke. Hooke regarded the compartment and the cell wall as the fundamental structure, and although he observed the protoplasmic contents, he thought of the living contents only as a "nourishing juice." It is now known that the cell wall is a characteristic part of the plant cell and a significant structural feature in plant tissues. Physiologically, however, the wall is of less importance than the living portion of the cell. The cell wall is, in fact, generally regarded as a product of the activity of the living cell. The living cell builds the wall around itself. The term cell is now properly applied to the living protoplasmic unit together with the cell wall. The living part of the cell has been called by various names, but the term protoplast is the one generally used.

THE PROTOPLAST

The General Material of the Protoplast—Properties of Protoplasm. The term protoplast is applied to the organized living unit of the cell as distinguished from the cell wall (Fig. 4). The material composing the protoplast is the **protoplasm**, a general term including living material of the whole plant

or animal body. Protoplasm may be looked upon as the living substance of which organisms are made; the protoplast, as the living unit of a single cell. Protoplasm, although composed of proteins, carbohydrates, fats, mineral matter, water, and other compounds, is more than a mere mixture of chemical compounds; it is itself an organized substance. Huxley referred to protoplasm as the "physical basis of life." This phrase, while possibly not quite expressing the modern concept of protoplasm, was a brief method of stating that many vital physiological processes take place in the protoplasm. All the physiological processes of the plant ultimately are associated with the protoplasm.

The physical and chemical properties of protoplasm have been the subject of many investigations which as yet have led to no certain conclusions fully accepted by all biologists. Although the general physical qualities of protoplasm are easily seen, its ultimate structure is unknown, owing to the difficulty of investigating the living substance. This difficulty has led to the conflicting conclusions of the various investigators. Protoplasm is hyaline in color, granular or foamy in appearance, and fluid, semifluid, or viscous in nature. The granular features probably depend upon inclusions of food particles, waste products, and other materials, while the fluidity is dependent upon the relative amounts of water in the protoplasm. The amount of water varies from 5 to 95 per cent. Investigations indicate that protoplasm is a very fine colloidal emulsion that is changeable, the changes being reversible.

Investigations of the structure of protoplasm have been stimulated in part by the desire of biologists to find the ultimate particles of life or the actual living material if such material exists. In the higher plants and animals, the protoplasm is divided into cells that are the structural and physiological units. According to the modern conception of "the physical basis of life" the whole mass of protoplasm in an organism is the actual seat of life. The organization, cooperation, and adjustment to one another of cell parts, of entire protoplasts, and finally the complete action of the whole organism constitutes life. From this viewpoint, the seat of life is not to be sought in any ultimate living particles.

Physiological Properties of Protoplasm. Perhaps the most outstanding features of protoplasm are its physiological properties because these characteristics distinguish living from nonliving things. They involve **metabolism, regulation, irritability, growth, and reproduction**. Only living protoplasm has these properties. They are discussed at greater length later in the text, but a brief indication of what they imply may be given here. **Metabolism** is the sum of the physiological processes in the building up and tearing down of protoplasm. It includes all the chemical changes which take place in the normal functioning of living matter, including the syn-

thesis of organic substances, digestion, respiration, and finally **assimilation**, which is the making of living out of nonliving material. **Regulation** refers to the ability of protoplasm to regulate the speed of its own physiological processes. That is, there is within the protoplasm the element of regulation whereby the various chemical processes proceed in orderly fashion and at ordinary temperatures. **Irritability** implies the ability of protoplasm to respond to external stimuli, such as light, temperature, gravity, and chemicals. The response may be a single movement or it may involve more complicated changes in the protoplasm. **Growth** involves not only increase in mass or volume but also development, *i.e.*, differentiation or change in form which only living protoplasm can achieve. It results in a progressive change from a less mature to a more mature condition and is irreversible. Finally, **reproduction** refers to the ability of protoplasm to reproduce itself.

The Structure of the Protoplast.

A typical plant cell consists of the living protoplast with all its parts and the surrounding cell wall. Generally, protoplasts are differentiated into **nucleus** and **cytosome**, which are recognizable as definite cell parts (Fig. 4). The term nucleus figuratively means the center, and it is in a sense the center of activity within the cell. The term cytosome is

derived from the words *cyte* and *soma* meaning "cell" and "body," respectively. Thus the term cytosome literally means the cell body. Structurally the cytosome has greater mass than the nucleus and occupies a larger part of the cell. The nucleus is located within the mass of the cytosome but is separated from the latter by a membrane or boundary.

As mentioned above, the protoplast is made up of the material protoplasm. The portion of the living protoplasm within the nucleus is known as the **nucleoplasm**. Similarly, the material composing the living parts of the cytosome is known as the **cytoplasm**. The terms nucleoplasm and cytoplasm thus refer to protoplasm located in different parts of the protoplast.

The Nucleus. General Features. Each typical protoplast contains a single conspicuous body called a nucleus (Fig. 4). In certain of the lower forms of plant life, diversity occurs in this regard. In the blue-green algae,

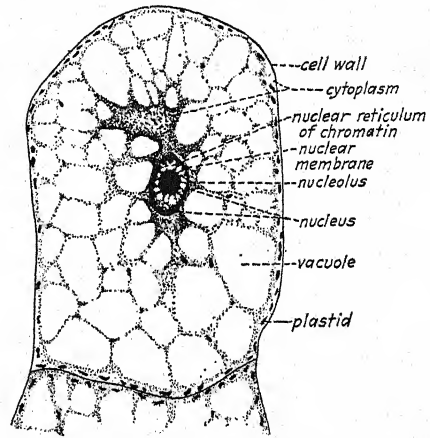


FIG. 4. Apical cell showing protoplasmic structure, from *Stypocaulon*, one of the brown algae.

for example, the protoplast is without a definite nucleus although there is presumably corresponding nuclear material present. In certain other species of algae and in some fungi, a multinucleate (coenocytic) condition is normally found. In seed plants, certain cells rendered abnormal by age, disease, or injury and certain reproductive cells are multinucleate. Subject to notable exceptions, however, each cell normally has a single nucleus.

The nucleus is composed of a denser material than the surrounding cytoplasm. This greater density is revealed by investigations involving microdissection of the cell, in which it has been found that the nucleus can be pushed about through the cytoplasm. In certain species of plants, it is sufficiently firm and rigid to permit a section to be cut from it while the remaining portion maintains its shape.

The nucleus is typically spherical or ovoid in shape, but the shape of the cell influences the nucleus to such an extent that many variations from the typical shape are to be found. In general, there may be a direct relationship between the size of the nucleus and the size of the cell, but this relationship is not always found. As the cell increases in size, there is not a corresponding increase in size of the nucleus. The nucleus therefore occupies relatively less space in mature cells. Although nuclei vary in size from $1\ \mu$ ($1/25,000$ in.) to $600\ \mu$ in diameter, their average size in plant cells could probably be stated to be 10 or $15\ \mu$ in diameter.

The Structure of the Nucleus. The structures and materials of the nucleus are the **nuclear membrane**, the **nuclear sap**, or **nuclear gel** (**karyolymph**), the **nuclear reticulum** made up of **chromatin**, and the **nucleoli** (Fig. 4).

The nucleus is separated from the cytoplasm by a membrane, called the **nuclear membrane**. Possibly it is best to regard the nuclear membrane as a morphological structure formed by the action of the nucleoplasm. The membrane surrounding the nucleus during its resting stage disappears at the time of nuclear division, and new membranes are formed when the new daughter nuclei are organized.

The body of the nucleus within the nuclear membrane is made up of a dense jelly-like mass which is apparently composed of at least two substances, each of which is known to be of complex chemical composition, viz., the **nuclear gel**, or **karyolymph**, and the **chromatin**. The nuclear sap, or nuclear gel, is the more abundant of the two substances. It apparently varies in consistency in various plants and under different conditions. The chromatin material appears to be dispersed through the nuclear gel in the form of a much distended network, or **reticulum** (Fig. 4). This network of chromatin seems to be suspended in or supported by the nuclear gel. The chromatin is regarded by many biologists as the most important constituent of the nucleus because of its importance in modern concepts of the physical basis of heredity.

When the nucleus divides, the chromatin becomes aggregated into definite rod-shaped bodies called **chromosomes** (Fig. 5, C, D). It is the behavior of these chromosomes that constitutes the essentials of nuclear division, a subject which forms the topic of a later discussion. The evidence of modern genetical studies tends more and more to show that the chromosomes can properly be regarded as the bearers of the hereditary material which passes from one generation to another. The constancy of the shape and number of chromosomes and regularity in the method of separation and splitting in nuclear division emphasize the importance of these units in the life history of an organism. It is now generally believed that hereditary factors occur in the form of units called **genes** which are located in the

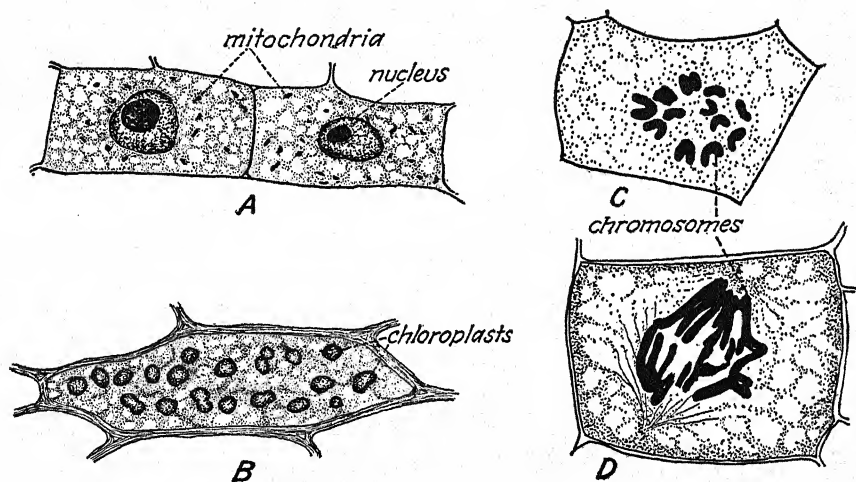


FIG. 5. Cells. A, cells showing nucleus, cytoplasm, and mitochondria; B, cell of moss leaf with chloroplasts; C and D, cells of root tip, showing chromosomes during nuclear division.

chromosomes. Although genes are of ultramicroscopic proportions, observation and study of certain structural features of chromosomes, visible during the early stages of nuclear division, tend to confirm the assumption about the location of genes in the chromosomes. The biological importance of genes can hardly be overestimated. They are the factors in the chromosomes which are effective in the development of many characters or characteristics of the organism. Their actions and interactions condition the development of hereditary traits. While normally stable, genes may change or mutate. Mutations are the building stones of evolution in living organisms.

In addition to the nuclear gel and chromatin, structures known as **nucleoli** are present in the nucleus. Often there is a single nucleolus in a nucleus, but the number varies in different cells. The structure of the

nucleolus varies considerably, but it is frequently characterized by a dense, heavy-staining interior surrounded by a lighter staining external layer (Fig. 4). Although the function of the nucleolus is unknown, it seems to be a mass of accumulated material, related to the metabolic changes in the nucleus.

The Function of the Nucleus. Investigations and observations tend to confirm the opinion that the nucleus is the center of physiological activity and that it plays an important if not predominant role in cell division and heredity. If a certain part of the cell is growing, the nucleus can be found there. This relationship is shown in the production of root hairs from epidermal cells of the root. The root hair develops opposite the nucleus in the cell, and the nucleus passes out into the growing hair. It has been found that cells deprived of their nuclei do not live long, although certain of the vital processes may continue for some time without the nucleus. This further emphasizes the significance of the nucleus to the protoplast as a whole.

The Cytosome. The cytosome is the second of the two principal parts of the protoplast. As mentioned earlier, the material composing the cytosome is the cytoplasm or the portion of the general protoplasm exclusive of the nucleus. Cytoplasm varies somewhat in density but is in general more fluid than the nucleoplasm and, in a young cell, is about the consistency of a soft jelly. Evidence of the fluid nature of the cytoplasm is furnished by its movement, which is called **streaming** and which is rapid enough to be observable in some plant structures (Fig. 6, A). The earlier discussion of the nature of protoplasm is applicable to cytoplasm. There are sometimes discernible two differentiated regions of the cytosome, an outer portion called the **plasma membrane**, or **ectoplast**, and an inner portion called the **endoplast**.

The Plasma Membrane, or Ectoplast. The extreme outer portion or periphery of the cytosome is organized into a definite limiting portion which lies next to the cell wall, when a cell wall is present, and in plant cells it is usually called the **plasma membrane**. This membrane separates the protoplast from its immediate environment. It is sometimes recognizable by its clear appearance as distinguished from the more granular endoplast and is thought to differ from it in physical nature. It has been described as a concentrated gel. Probably the best concept is that the plasma membrane is composed of a dense colloidal emulsion of proteins, fats, and water. Because of its semipermeable nature, the plasma membrane is an exceedingly important structure of the protoplast in relation to the absorption and loss of water and other substances by the cell. The physical processes involved in the intake and outgo of water are discussed later, but it is well, at this point, to emphasize the connection of the plasma membrane with

these processes. All osmotic action, as well as the absorption of inorganic and organic substances by the cell, depends upon the permeability of the plasma membrane. In lower organisms, the ectoplast is also of importance in giving rise to certain structures of the cells such as the cilia and flagella of motile forms; these are said to be ectoplasmic strands.

The Endoplast. The **endoplast** is the more granular, inner portion of the cytosome. Often the granular appearance is emphasized by the presence of inclusions of particles of food materials, mineral crystals and other substances.

The Plastids. **Plastids** are prominent and important structures which to a considerable degree have an independent existence in the mass of the cytosome. They are of several different types, each associated with a definite physiological function and often distinguished by a specific color. Emphasis should be placed upon the plastid as a definite protoplasmic body rather than upon its color. The body of the plastid is called the **stroma**. Plastids probably arise by division of preexisting plastids just as nuclei arise from nuclei and are never made *de novo* (anew) in the cytoplasm. Dividing plastids can easily be seen in thin moss leaves and in algae. Plastids are of several kinds, *viz.*, **leucoplasts**, which are colorless, **amyloplasts**, which are leucoplasts containing starch, **chloroplasts**, which contain chlorophyll and carotenoid pigments, and **chromoplasts**, which contain carotenoid pigments in the absence of chlorophyll pigments. Frequently regarded as plastids are the **eyespot**s, which are bright-colored, generally red, bodies regularly present in the motile algae and in the reproductive cells of many of the higher algae.

The **leucoplasts** are of two kinds, small and large plastids. The small ones seem to develop into the larger types and also into the chloroplasts and chromoplasts. Leucoplasts of the larger type are known as **amyloplasts** (starch formers) and function in the deposit of starch for storage purposes or reserve starch. This starch is formed from elaborated carbohydrates and is deposited within the body, or stroma, of the amyloplast.

The **chloroplasts** are the green-colored plastids (Fig. 5, *B*, and frontispiece). These plastids frequently originate from the small leucoplasts, the green color developing under the action of sunlight and other factors. The chloroplasts are the most important of the plastids because of the presence of the green chlorophyll pigments (already described in Chap. 2), which are associated with the process by which carbohydrates are formed. The chloroplasts of the higher plants are very small, spherical, ovoid, or disk-shaped bodies. In the algae, they are frequently quite large and in some groups are of unusual shapes, such as the radiate plastids of *Zygnema* and the elaborate spiral bands of *Spirogyra* (Fig. 143).

The orange, yellow, and red plastids, called **chromoplasts**, owe their color

to the presence of carotenoid pigments and are commonly found in many fruits and flowers (frontispiece). In some cases the chromoplast develops from the chloroplast. This is said to be true of the tomato fruit. In this case, the same plastid passes through the three stages—leucoplast, chloroplast, and chromoplast. In the tomato flower, the ovary of the pistil, which develops into the fruit, contains only leucoplasts; later the green tomato contains chloroplasts developed from the colorless plastids, and when the fruit ripens these chloroplasts develop a red or yellow color. In a half-ripe tomato two kinds of plastids, green and red, can be observed. In such cases, the red or yellow pigments seem to bear about the same relationship to the stroma of the plastid as the green pigment in the case of

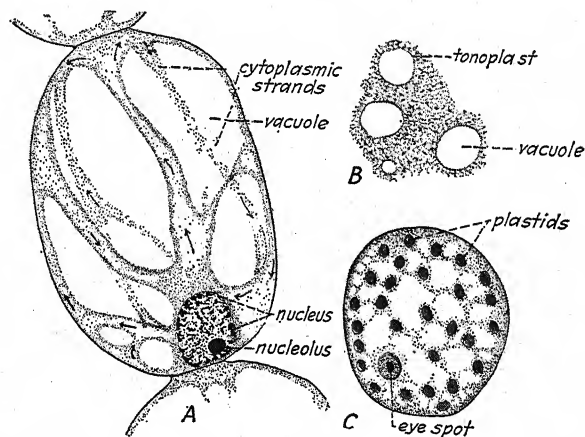


FIG. 6. Structure of the cell. *A* and *B*, the structure of protoplasm; *A*, cell from a stamen hair of *Tradescantia*, the arrows indicating direction of streaming cytoplasm; the granules in the cytoplasm were observed to move at the rate of 10μ per second; *B*, vacuoles and structure of the cytoplasm in the egg of *Ceratophyllum*, a gymnosperm; *C*, zoospore of *Culleria* showing the eyespot and plastids.

the chloroplasts. In other chromoplasts, the pigment appears in the form of crystals.

The **eyespot** of the lower plants seems to be a plastid (Fig. 6, *C*). In some genera, it certainly has a stroma and pigments. In many cases, regardless of its questionable function as an organ sensitive to light, it is a specialized sort of plastid. In other cases, the evidence for the plastid nature of the eyespot is not so clear.

Chondriosomes, or Mitochondria. Certain very small bodies called **chondriosomes**, or **mitochondria**, have been found to be almost universally present in the cytoplasm of both plants and animals (Figs. 5, *A*; 7, *A*). While they are very abundant, they are not easily demonstrated except by the use of special methods of preparation because of their characteristic

staining reactions. Chondriosomes have been described as "substances which occur in the form of granules, rods, and filaments in almost all living cells." Their functions in the cell are not well known, and conclusions regarding them vary and are often contradictory. Considerable evidence shows that in some instances they originate by division of preexisting chondriosomes much as in the case of plastids. It is possible that the group of objects termed chondriosomes is a diverse collection of bodies having various origins and performing various functions.

Vacuoles. Within the body of the cytosome there are usually one or more sap cavities, or **vacuoles**. Vacuoles are of two kinds, **water vacuoles** (Fig. 6) and **oil vacuoles**. The so-called water vacuoles contain a solution of organic and inorganic substances, collectively called the **cell sap**. Young cells are likely to contain many small water vacuoles. As the cells increase in size, the vacuoles continue to enlarge until finally they become confluent. In mature cells, therefore, there is likely to be one large vacuole in the center of the cell with the cytoplasm occupying a peripheral position against the cell wall (Fig. 51). The materials in solution in the cell sap may include anthocyanins, flavones, organic acids and their salts, inorganic compounds, sugars, and many other substances. Each water vacuole is surrounded by a modified layer of cytoplasm called the **tonoplast** (Fig. 6, *B*). The tonoplasts may be regarded as cytoplasmic membranes separating the contents of the vacuoles from the cytoplasm proper and are perhaps similar in function to the plasma membrane of the cell. The oil vacuoles are droplets of oil and never attain the large dimensions of water vacuoles.

Miscellaneous Inclusions. A considerable variety of nonliving materials is included in the cytosome. Some of these are carried in the body of the cytosome while others are localized rather definitely in the vacuoles. Most of these inclusions are of the nature of food, either reserve food or foods in transit from one part of the cell or organism to another, and practically all of them can be thought of as the products of the physiological activity of the cell. Fat and oil globules, starch, protein, crystals of calcium oxalate, calcium carbonate, and silica are common inclusions. These materials exist in all conditions from solutions to deposits of granular material. If in solution, they are found in the cell sap of the vacuoles.

Other Cytosomic Bodies—Centrosome. The **centrosome** is a minute deep-staining body regularly present near the nucleus in animal cells, in the cells of such lower plants as algae and fungi, and in the reproductive cells of some other forms. The centrosome is associated with nuclear division, in the course of which it divides and the new centrosomes pass to the poles of the spindles, each forming the center of cytoplasmic radiations called the "asters." In the motile reproductive cells, the centrosome is often associated with the formation of the cilia, which are the organs of locomotion of these structures. It seems that centrosomes are not always permanent cell parts, as are plastids and nuclei or perhaps even the chondriosomes, but that certainly in many

cases they arise anew in the cytoplasm, probably as a result of the physiological activity at the time of cell division.

Blepharoplast. The term blepharoplast has been quite generally applied to the structure from which the cilia arise in the motile male cells, or sperms, of plants. The manner of origin and the ultimate structure of the blepharoplast vary greatly in the different groups of plants. In most of the plants investigated it originates as a centrosome-like body which generally undergoes some modification (Fig. 7). Ultimately the

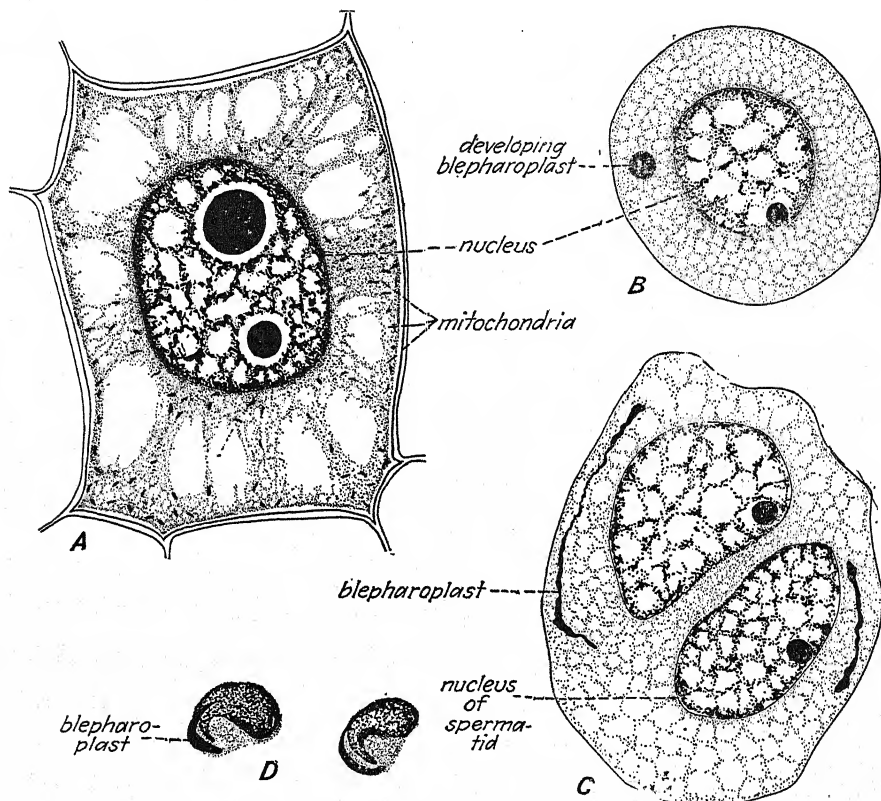


FIG. 7. Cytosomic bodies. A, cell of *Narcissus* root tip with chondriosomes (mitochondria); B and C, development of the blepharoplast in *Ceratozamia* sperms; B, young sperm mother cell with developing blepharoplast; C, older stage of *Ceratozamia* sperm mother cell with larger blepharoplasts and sperms; D, sperms of *Equisetum* showing mature blepharoplasts.

structure assumes a form and position suitable for the cilia of the motile cell. The cilia at maturity appear attached to the blepharoplast.

Golgi Bodies, Cytosomic Canals, and Related Structures. The presence of other types of cytosomic inclusions has been successfully demonstrated by special methods of preparation. These were first noted and have been more extensively studied in animal than in plant cells. Cells from the nervous system and secretory tissues such as stomach epithelium, treated by these special methods, show a more or less conspicu-

ous net-like body or structure variously termed dictyosome, or Golgi body, Golgi canals, Golgi material, or Golgi apparatus for its discoverer Golgi (Fig. 8, A-C).

More recently, studies of plant tissues have been undertaken, using similar methods of preparation, in order to learn if there are corresponding cytosomic inclusions in plant cells. As a result of these studies, certain cytosomic structures have been found which have been compared with the Golgi bodies of animal cells. These rather recent additions to the list of cytosomic inclusions in plant cells are, to date, of three types, *viz.*, cytosomic canals, demonstrated by Bensley as early as 1910; a net-like structure in young plastids of moss plants, demonstrated by Weier in 1932; and certain small plate-like, or disk-shaped, bodies termed "Osmiophilic platelets" by their discoverer Bowen (Fig. 8, D). While there is no question as to the presence of these cytosomic inclusions, there is considerable confusion at present concerning their nature and function. It is uncertain whether these are actual living structures or merely non-

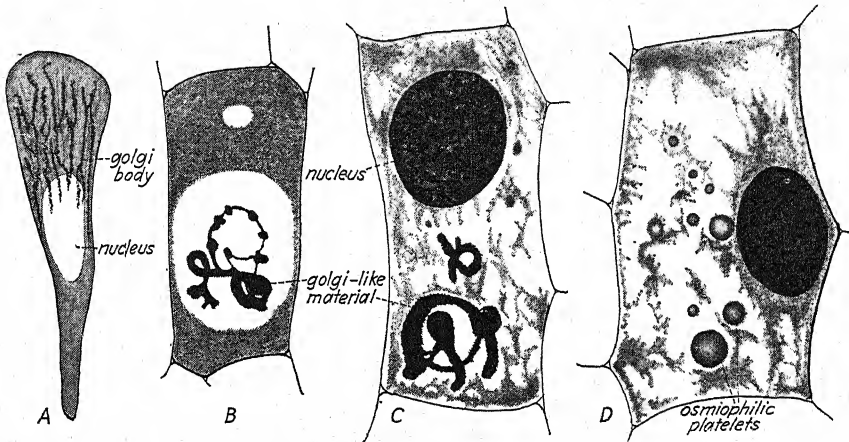


FIG. 8. Golgi bodies and other cytosomic materials. A, reticulate Golgi body in stomach epithelium of animal; B and C, Golgi-like material in cells of lily root tip; D, osmiophilic platelets in root-tip cell of *Allium*. (B, C, and D redrawn from McIlvaine in *Proc. Penn. Acad. Sci.*, 1934.)

living material massed in the cytoplasm and rendered visible by the staining methods. While the Golgi bodies in the secretory cells of animal tissue may have a function closely associated with the secretions characteristic of those cells, the functions of the comparable structures in plant cells are even more in doubt. With the ultimate nature and function in each case in doubt, definite comparisons of these plant cytosomic inclusions with the Golgi bodies of animal cells on any basis excepting general appearance becomes exceedingly difficult.

THE CELL WALL

The cell wall is the result of the activity of the protoplast, *i.e.*, it is built up by the protoplast. The presence of rigid cell walls is the primary structural characteristic of plant tissues. Animal cells have no such walls but generally only delicate, limiting membranes surrounding the protoplasts.

In young tissues, the cell wall consists of a single layer, while in older tissues it is composed of two or more layers. The wall of a young cell is called the **primary wall**, or layer. The additional thickenings are known as the secondary or tertiary layers or, collectively, the **secondary thickenings**. When these secondary thickenings are formed, the primary layer is usually referred to as the **middle lamella**. Secondary thickenings are often laid down on the primary cell wall in an uneven manner, especially in walls that become greatly thickened. Thin places known as **pits** are left in such walls. These are sometimes distributed in a very uniform pattern over the wall of the cell. In some cells, the later thickening overhangs the border of these thin places, and the pits are then known as **bordered pits** (Fig. 12, *B*). Pits without such overhanging borders are known as **simple pits**.

Cell walls are composed of various substances. The primary cell wall or middle lamella usually consists of **pectic materials** such as calcium pectate. Pectic materials are hydrophilic colloids, *i.e.*, colloids that are able to absorb and hold water. The outer walls of root hairs also consist of these materials. Of the substances found in the secondary walls, **cellulose** is by far the most common. Cellulose is so universally found in the cell walls of plants that it is considered a distinguishing feature of plants. It is cellulose that makes plant-cell walls more or less rigid, as opposed to the pliable walls of animal cells. Cellulose walls are readily permeable to water and to most of the substances dissolved in the water found in plant cells. Cellulose is usually found in plant-cell walls no matter what other substances may be present. Cell walls sometimes contain **hemicelluloses**, which are complex organic compounds related to cellulose but not so insoluble. They make the walls tough. They are found in the walls of the cells of some seeds and in other parts of the plant.

The cell walls of the woody parts of plants are strengthened by a complex organic substance called **lignin**. Lignin makes walls tough and hard, but it does not prevent the passage of water and the substances dissolved in water. Cells that have been strengthened by the addition of lignin are said to be **lignified**. Lignin replaces the pectic substances in the middle lamellae of wood cells and to some extent is added to the cellulose content of the secondary thickenings. It is the combination of lignin and cellulose that gives wood many of its properties.

Cutin and **suberin** are closely related waxy substances found in the walls of cells that are exposed to the atmosphere. Cutin is restricted to epidermal tissues, such as those found on leaves, young stems, flowers, and fruits, while suberin is found only in cork cells of the stem, root, or other plant organ. Both of these substances render cells waterproof, thereby preventing water from escaping through them from the interior of the organ on which they are found.

In addition to the substances already mentioned, many different kinds of inorganic materials are sometimes found in plant-cell walls. Some of these cause the walls to become very hard and brittle.

Plasmodesmi.¹ The protoplasts of adjacent cells are sometimes connected by means of extremely fine strands of cytoplasm extending through the cell walls. These strands are known as **plasmodesmi** (singular, **plasmodesmus**) (Fig. 9). In ordinary cells, they are usually so fine as to be entirely invisible under the microscope unless a special technique has been used to bring them out. They are most often seen in the cells of ferns and gymnosperms and in the walls of endosperm, which is a food-storage tissue found in some seeds. Though seldom seen, they are thought to be present generally in living plant cells.

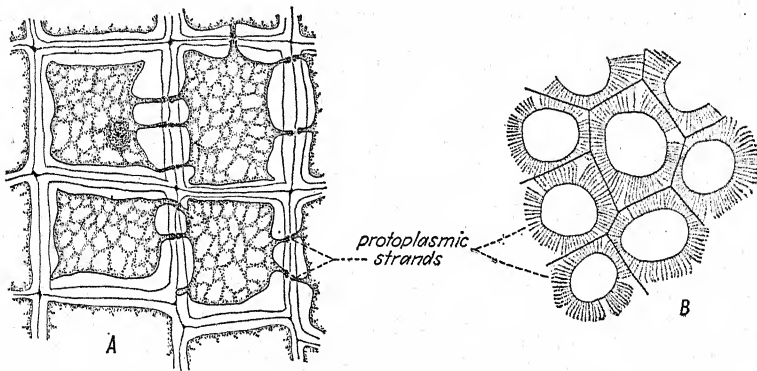


FIG. 9. Plasmodesmi. A, in walls of parenchyma cells in stem of *Cryptomeria*; cytoplasmic contents of the cells are contracted, emphasizing the presence of the cytoplasmic strands passing through small openings in the walls; B, in walls of endosperm of *Diospyros*. (Drawings by Helen Deuss Hill.)

TYPES OF CELLS—TISSUES

In the simplest plants, the whole plant body consists of but a single cell or a colony of cells all essentially alike. Since plants of this kind usually live submersed in water, each cell is in direct contact with its supply of minerals, water, and other requirements and hence is independent of other cells. There is little difference between the cells as to form or function. In the more complex plants, and particularly in plants growing on land, a "division of labor" occurs among cells, some having one function and others another. There are thus developed specialized tissues and organs made up of many different kinds of cells, which show considerable variation in size, shape, general characteristics, and function.

¹ These structures are often called **plasmodesmata** (singular, **plasmodesma**).

It is in the seed plants that the greatest diversity of form and structure of the plant body occurs. In such plants no one organ is independent of the others but all work together in performing the life functions of the plant as a whole. This is accomplished by a high degree of specialization in the cells and by the development of a highly complex system of tissues.

A **tissue**, in the most general use of the term, may be looked upon as a group of similar cells performing a common function. Such a tissue is commonly called a **simple tissue**. Often, however, the term is applied to a more complex group of cells, some of which may differ markedly from others in both form and function, but all of which work together as a unit. These might be referred to as **complex tissues**. This is true of such tissues as the phloem and the xylem, described later. The name of a simple tissue is often applied also to the type of cells of which the tissue is

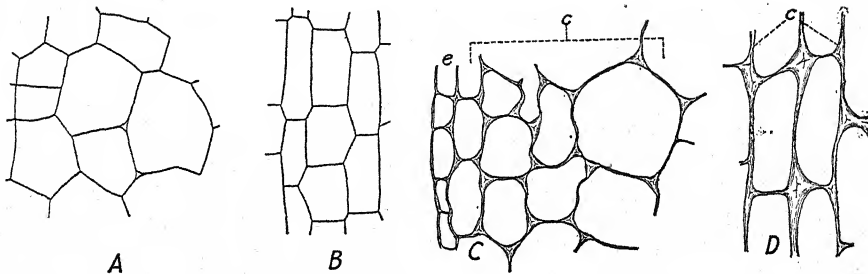


FIG. 10. A and B, parenchyma cells of balsam plant (*Impatiens Sultanii*); A, in cross section; B, in longitudinal section; C and D, collenchyma cells of the same plant; C, in cross section, with *e*, epidermal layer, and *c*, collenchyma region; D, in longitudinal section. (Drawings by F. Brown.)

composed. This is true of parenchyma, collenchyma, and sclerenchyma, all of which are simple tissues described in the following paragraphs.

Parenchyma. Of the usual types of cells and tissues found in plants parenchyma is the most common if not the most abundant. It is the basic type from which all other kinds of cells are derived. Parenchyma tissue (Fig. 10, A-B) consists typically of thin-walled cells that are approximately isodiametric, *i.e.*, not much longer than they are wide. The individual cells may be spherical, cubical, many-sided, frequently with 14 faces, irregular, or of other forms. They usually contain a living protoplasmic content and retain their capacity to divide even though division may never occur after the cells are mature. The parenchyma cells of the growing tips of roots and stems are known as **meristematic tissue**. These cells are in an active state of division, giving rise, through modification, to the primary permanent tissues of the plant.

Parenchyma cells are found in all organs of the plant. They function in

food synthesis, food storage, and in other ways. When parenchyma tissue contains chloroplasts, it is called **chlorenchyma**. The **epidermis**, which is the outermost layer of cells of young stems, young roots, leaves, flower parts, and fruits, consists of somewhat modified parenchyma cells.

Collenchyma. Collenchyma tissue (Fig. 10, *C-D*) is made up of somewhat elongated cells with cellulose thickening occurring as longitudinal strips on the walls, usually confined to the corners of the cells. The cells usually have a protoplasmic content and hence remain alive at maturity. Collenchyma is commonly found immediately beneath the epidermis in the outer parts of herbaceous stems and in the petioles and midribs of leaves. It is chiefly a temporary supporting tissue, developed before the principal supporting fibrous tissue of the stem is differentiated.

Sclerenchyma. Extreme thickening and hardening of the walls of parenchyma cells result in the formation of a stony or fibrous tissue called sclerenchyma. Sclerenchyma cells are characterized by simple or unbordered pits. The walls are very hard and are often so thick as to leave only a very small cavity within the cell. These cells, when mature, die and lose their protoplasmic contents. They function chiefly in strengthening and support of the stem and in the protection of softer internal tissues. There are two principal kinds of sclerenchyma cells, *viz.*, **stone cells** and **sclerenchyma fibers**. The **stone cells** (Fig. 11, *E*) are of many irregular shapes but not much longer than they are wide. Stone cells may occur singly or in groups. They occur in many parts of the plant but particularly in fruits and seeds. The shells of nuts contain many stone cells. The grit commonly present in pears consists of stone cells. **Sclerenchyma fibers** (Fig. 11, *C-D*) are greatly elongated cells, usually with pointed or tapering ends and generally with unbordered pits in the walls. They differ in this respect from other fiber cells found in the wood. Sclerenchyma fibers are usually dead cells with very small cavities, owing to the extreme thickening of the wall. They often occur in groups forming longitudinal strands that are very efficient strengthening elements in the stem. Rope and linen are made from the sclerenchyma fibers of plants, chiefly from hemp and flax, respectively. Sclerenchyma fibers are named according to the part of the stem in which they occur. Thus there are epidermal fibers, cortical fibers, pericycle fibers, and phloem fibers.

Xylem and Phloem. The stems of plants consist of several general regions as epidermal, cortical, and conducting, or vascular, regions. The conducting region is made up of a **phloem** portion and a woody portion or **xylem**. The phloem makes up a part of the general region of the bark of plants and the xylem is the wood. The conducting, or vascular, region extends from the roots through the stem to the leaves, flowers, and fruits. Associated as it is with the function of conduction, the vascular system of

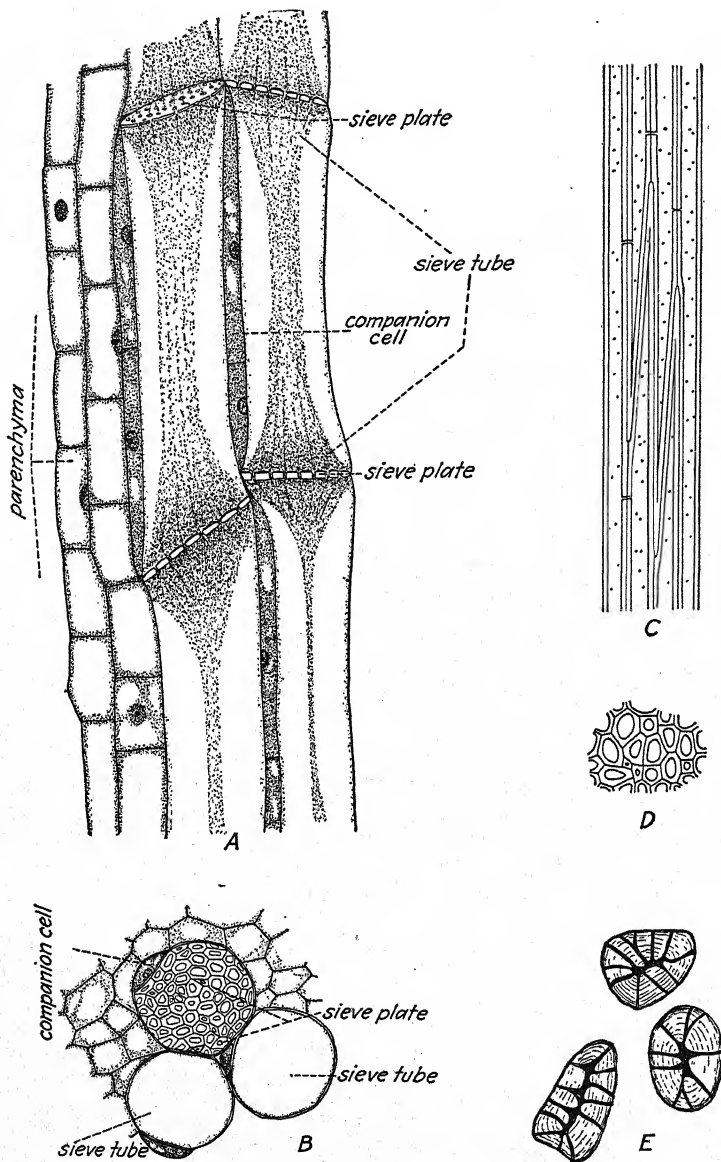


FIG. 11. A and B, longitudinal and cross sections through the phloem region of the stem of *Tetracera*, showing structure; C and D, longitudinal and cross-sectional views of sclerenchyma fibers from the pericycle of the ash stem (*Fraxinus*); E, stone cells from fruit of pear. (Drawings by F. Brown.)

plants shows many modifications of cells and in it are found many cell types.

Xylem. The cells composing the woody, or xylem, portion of plants have undergone the most extreme modifications of all the cells in plants. Cells of the wood are greatly elongated and have considerable thickening of the walls. The manner and extent of the thickening in these xylem cells are extremely varied and have, therefore, resulted in some very elaborate

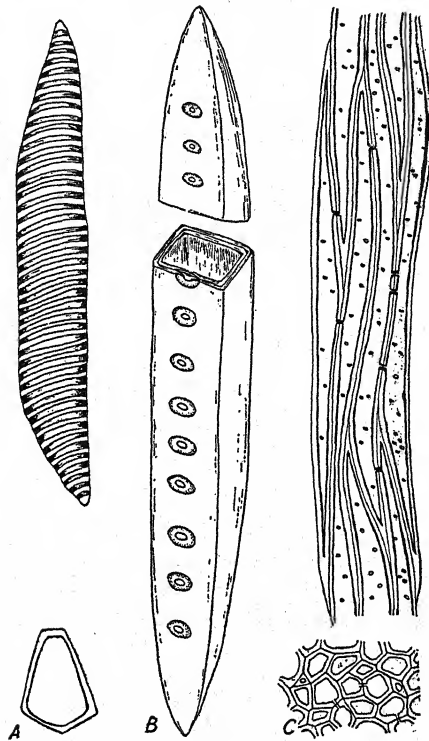


FIG. 12. A, cross-sectional and longitudinal views of a tracheid from the stem of a fern (*Onoclea sensibilis*); B, a tracheid with bordered pits from the stem of white pine (*Pinus Strobus*); C, wood fibers of the ash stem (*Fraxinus*) in cross and longitudinal sections. (Drawings by F. Brown.)

patterns of cells. The kinds of cells composing the xylem vary in different plants but may consist of **parenchyma**, **tracheids**, **vessels**, or **tracheae**, and **wood fibers**. **Xylem parenchyma** is much like ordinary parenchyma, though often somewhat thicker walled, and is used chiefly for food storage. The **wood ray cells** are also parenchyma. The **wood fibers** (Fig. 12, C) are similar in structure to the fibers already described and are used for strengthening and support. They are characterized by having bordered

pits. **Tracheids** (Fig. 12, A-B) are elongated dead cells with tapering ends and a fairly large cavity, or lumen. The walls are somewhat thickened and are usually pitted. Tracheids are thus of such structure as to be able to function in both conduction and support. The wood of pines is made up almost exclusively of tracheids.

The **tracheae**, or **vessels**, are chains of cylindrical, elongated dead cells attached end to end with the end walls usually dissolved, forming long tubes or ducts through which water and dissolved mineral salts are transported. The walls are variously strengthened on the inside by thickened rings

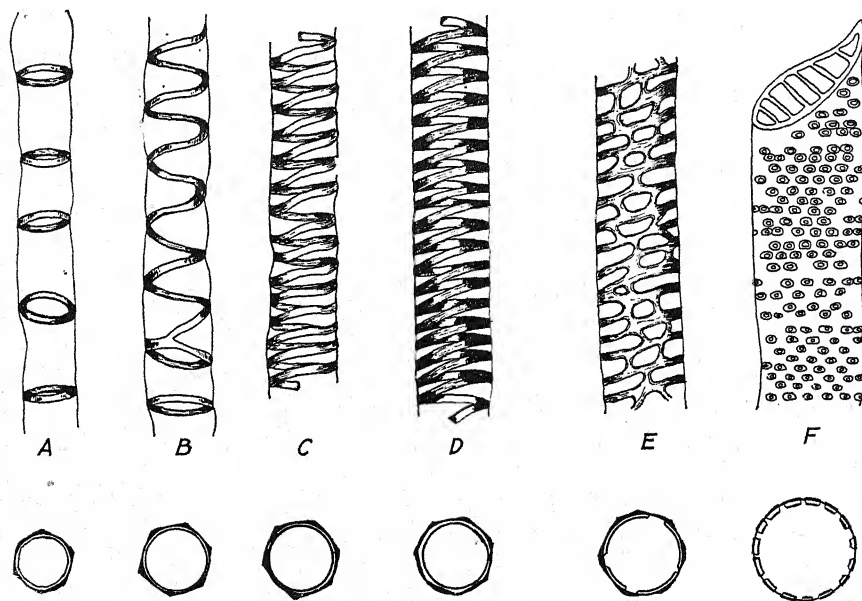


FIG. 13. Cross-sectional and longitudinal views of vessel segments. A, ringed vessel; B-D, spiral vessels; E, scalariform vessel; F, pitted vessel with scalariform end wall. A-D, from the stem of the balsam plant (*Impatiens Sultani*); E, from the stem of the sunflower (*Helianthus annuus*); F, from the stem of the alder (*Alnus*). (Drawings by F. Brown.)

(**ringed**, or **annular**, **vessels**) (Fig. 13, A), spirals (**spiral vessels**) (Fig. 13, B-D), or irregular transverse bars extending part way around the inside (**scalariform vessels**) (Fig. 13, E). In some vessels the wall is of more or less uniform thickness throughout except for the pits (**pitted vessels**) (Fig. 13, F). Tracheae are so highly specialized as to serve no other function save that of conduction. The xylem as a whole is the outstanding water-conducting and strengthening tissue of the plant.

Phloem. The cell composition of the phloem also differs in different kinds of plants, but may consist (in its greatest complexity) of **phloem**

parenchyma, fibers, sieve tubes, and companion cells. The first two types of cells have already been described. The most characteristic cell type of the phloem is the sieve tube. **Sieve tubes** (Fig. 11, A) consist of longitudinal rows of elongated, rather thin-walled, living cells with rather large cavities. The end walls are perforated, forming the so-called **sieve plates** (Fig. 11, A-B). In the more primitive types of plants, sieve plates also occur along the side walls of the sieve tubes. There is usually a large central vacuole in the individual cells and a thin peripheral layer of cytoplasm. The cytoplasm of adjoining cells is usually connected by strands extending through the sieve plates. Lying adjacent to the sieve tubes and connected with them by pores are usually one or more rows of smaller, elongated cells known as **companion cells** (Fig. 11, A-B). The companion cells are a modified type of parenchyma, filled with dense cytoplasm and a prominent nucleus. They are thought in some way to assist the sieve tubes in the conduction of foods. The chief function of the phloem is probably the conduction of such foods as sugars and proteins. There is some evidence that it may also function in the transport of inorganic substances.

THE TISSUE SYSTEMS

All the tissues found in plants may be grouped into three systems: the **epidermal tissue system**, the **fundamental tissue system**, and the **vascular tissue system**. The last two systems are not single tissues like those just described but are made up of groups of tissues.

The Epidermal Tissue System. The epidermal tissue system consists of the outer protective layer, or **epidermis**, covering leaves, young stems, young roots, and the parts of flowers and fruits. The cells composing the epidermis are modified parenchyma cells. Epidermal cells may be of very irregular shapes owing to the relative plasticity of the cell walls and the tension of the whole tissue. Each of the epidermal cells contains a protoplast consisting of nucleus and cytosome but, in most seed plants, lacking chloroplasts. In ferns, chloroplasts frequently occur in the epidermal cells. Stomata, which are pores used in gaseous exchange, occur regularly in the epidermis of leaves and young stems. The epidermis generally consists of a single layer of cells, but sometimes there are several layers, in which case it is called a **multiple epidermis**. Sometimes a specialized layer of cells, called the **hypodermis**, which usually has a different origin from that of the epidermis, is developed immediately beneath the epidermis. This layer is found in the leaves of many plants normally inhabiting dry regions.

Epidermal cells frequently show considerable thickening of the walls. On the outer cell wall there is usually a **cuticle**, which is a deposit of waxy material called cutin and which functions in keeping moisture within the plant body. The epidermis of stems which increase in diameter from season to season is broken and lost after a few years and its place as a protective layer is taken by a corky tissue developed beneath the epidermal layer.

The Fundamental Tissue System. The fundamental, or ground, tissue system, making up a major portion of the young root, the young stem, and the leaf, as well as the flower and the fruit, is composed chiefly of parenchyma cells. The internal tissues of the leaf belong almost entirely to this system. In the young root the fundamental

tissue system consists of the cortex and possibly the endodermis, while in the stem it is made up of the same tissues together with the pith. These individual tissues are described later in the chapters on the root and the stem. While the major part of these tissues consists of parenchyma cells, there are also found in them collenchyma and sclerenchyma cells.

The Vascular Tissue System. The third of the tissue systems is the vascular, a complex system, consisting chiefly of phloem and xylem and used for the conduction of water, mineral salts, and foods as well as for strengthening and support. In older perennial plants, the vascular tissue system makes up the major portion of the stem and the root. The arrangement of the vascular tissues varies in different organs of the plant as well as in different kinds of plants. The details of this system of tissues are described in the following chapters.

CHAPTER 4

LEAVES

ORIGIN AND EXTERNAL FORM

Leaves are perhaps the most conspicuous parts of plants. Being rich in chlorophyll, they are responsible for the common green color of forests and fields. They are always borne on stems. The part of the stem to which a leaf is attached is called a **node**. The upper angle the leaf makes with the stem at its point of attachment is called the **axil** of the leaf (Fig. 14). Invariably a bud is found in this axil, although the bud may be so immature as to be invisible to the unaided eye or it may be covered by a sheathing leaf base.

Leaves in general are characterized by their thin and expanded form. Though usually very thin, they are able to maintain their shape because of an internal framework, or skeleton, of more or less rigid **veins**. In size, leaves vary from tiny, almost microscopic structures to forms 10 to 20 ft. and more long. As will be seen later, leaves are the outstanding organs in which carbohydrate foods are made and hence are very important to the life of the plant.

Origin and Development of Leaves. In general, leaves arise in buds. Buds contain the undeveloped growing points of stems. In perennial plants, these growing points are often protected by a series of scale-like leaves that make the bud more or less conspicuous. The growing point itself is made up of cells that are all essentially alike. These cells are characterized by being thin-walled and isodiametric and by consisting of rather dense protoplasm with large nuclei. During the growing season they are practically all in an active state of division, forming new cells and causing the growing point to expand and move forward. Cells with these characteristics are known as **meristematic cells**. At regular intervals around the sides of the growing tip, certain cells of the outermost layers, by a series of divisions, form small outgrowths which are known as **leaf primordia** (Fig. 15, *b, c*). By the continued growth of these primordia, the leaves are developed. At first the growth is chiefly at the tip or apex of the primordium (apical growth), but later, especially in pinnately veined leaves, the sides of the primordium begin to enlarge rapidly by intercalary growth (*i.e.*, growth not restricted to the apex) to form the expanded portion of the leaf. Sooner or later, growth at the apex ceases, and further expansion of

the leaf takes place only at the base. All this development occurs while the leaf is still in the bud and before it has reached a length of more than a

few millimeters. When a leaf is large enough to be handled, the growing region can be demonstrated easily by marking the leaf into small squares with India ink and observing how these squares enlarge as the leaf grows (Fig. 16). The full development of the leaf often takes place in a comparatively short time. When the leaf has reached mature size, all growth ceases. In this respect leaves differ from roots and stems, which continue to grow as long as the plant is living.

In many perennial plants the new leaves are differentiated in the buds during the summer and go into a dormant state from which they emerge

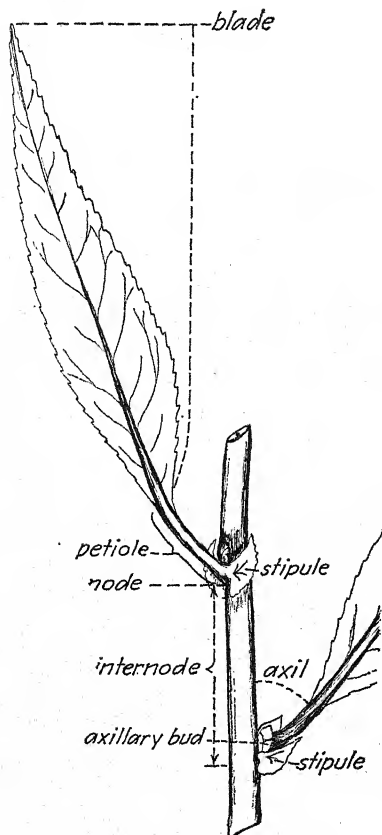


FIG. 14.

FIG. 14. Portion of a branch of willow showing parts of a complete leaf and the relation of the leaf to the stem. The upper angle, which the leaf makes with the stem, is called the leaf axil. (Drawing by F. Brown.)

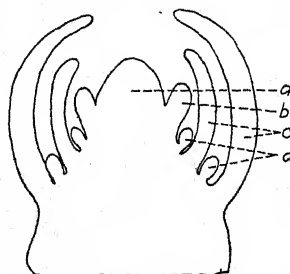


FIG. 15.

FIG. 15. Diagrammatic representation of formation of leaves from growing point. *a*, primordial meristem; *b*, leaf primordium; *c*, more fully developed leaves; *d*, axillary buds.

the following spring. In many of the monocotyledonous plants, basal growth of the leaves continues for some time and results in a long narrow form such as is common in the grasses. In the ferns, apical growth proceeds after basal growth has ceased. Such leaves keep unrolling at the tips until mature (Fig. 20, D).

The Parts of a Leaf. A complete leaf consists of an expanded portion known as the **lamina**, or **blade**, a leafstalk, or **petiole**, by which the blade

is attached to the stem, and two small appendages at the base of the petiole, called **stipules** (Fig. 14). When any of these parts are lacking, the leaf is said to be incomplete.

The Leaf Blade, or Lamina. The leaf blade is the most conspicuous and, in general, the most important part of the leaf. It is usually thin and is constructed in such a manner as to expose the greatest number of its chlorophyll-containing cells to light. The form or outline of the leaf blade, while constant for any particular species of plant, presents wide

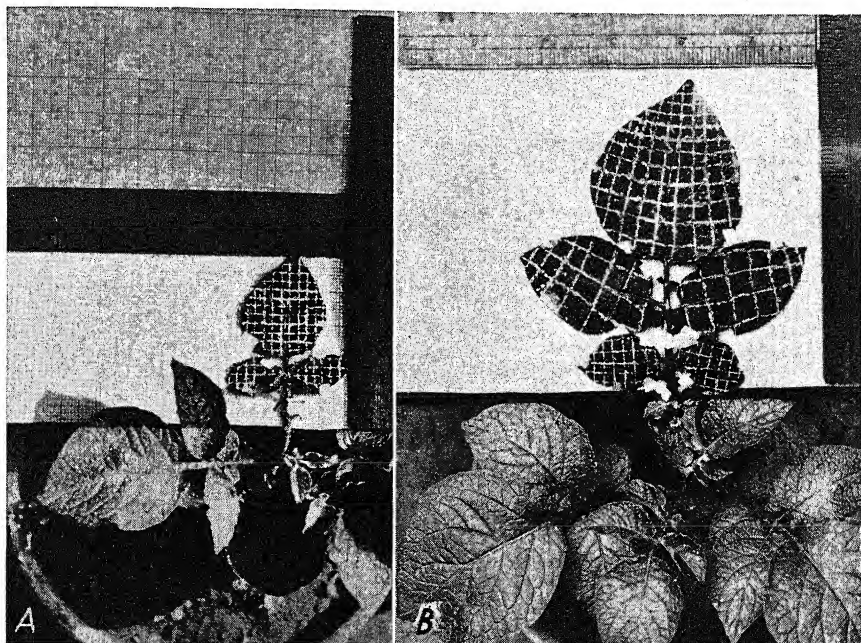


FIG. 16. Region of growth in the leaf of a dicotyledonous plant (potato). A, young leaf marked into $\frac{1}{8}$ in. squares; B, the same leaf as it appeared 10 days later. (Figure furnished by Dr. E. L. Nixon.)

variations. The different forms are usually described by such terms as linear, lanceolate, elliptic, ovate, orbicular, cordate, and reniform (Fig. 17, I). Likewise the margin of the leaf blade may vary from an entire, or even, condition, through all gradations, to deep sinuses extending almost to the middle of the blade. The various types of margins are designated by such terms as entire, undulate, crenate, dentate, serrate, and lobed (Fig. 17, II).

The Petiole. The petiole is usually a stem-like structure which connects the leaf blade with the stem (Fig. 14). It functions in conducting materials to and from the blade. Largely through the growth in length

or the bending and twisting of the petiole, the leaf blade is brought into a favorable position with respect to light. This position is usually broad-side toward the light, regardless of what may be the position of the stem

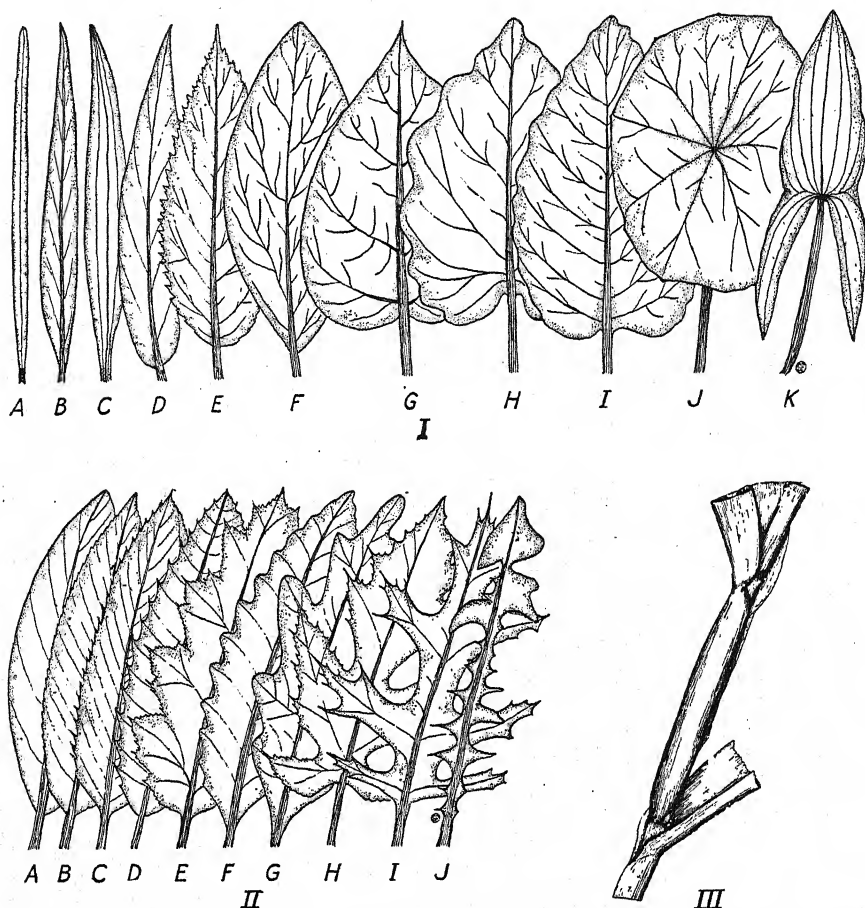


FIG. 17. I, forms of leaves. A, linear; B-D, lanceolate; E, elongate ovate; F, elliptical; G and H, cordate; I, ovate; J, peltate; K, sagittate. II, types of leaf margins. A, entire; B, finely serrate; C, sharply serrate; D, coarsely serrate; E, dentate; F, coarsely crenate; G-I, deeply lobed; J, pinnatifid. III, portion of stem of corn showing leaf sheaths extending from one node to the next lower one. (I and II drawn by Edna S. Fox; III drawn by Elsie M. McDougale.)

from which the leaf originates. It is best seen in climbing plants that grow over the sides of stone buildings. All the leaves of such plants usually lie in a plane nearly parallel to the side of the building. Usually the entire available space is covered with leaves in such a manner that they do not shade each other to any great extent. This is brought about

chiefly by the wide differences in the lengths and positions of the petioles of the different leaves. For the same reason, the leaves of a tree are all directed outward and present an entirely different aspect when viewed from beneath the tree from what they do when viewed at a distance.

The shape and form of the petiole vary in different species of plants. In some leaves petioles are absent. Such leaves are said to be **sessile** (Fig. 21, A). In many of the monocotyledonous plants, and especially in the grasses, the base of the leaf forms a sheath around the stem, usually extending from one node to the next lower one (Fig. 17, III).

Stipules. There are usually two stipules present at the base of the petiole (Figs. 14, 19, B), but some leaves, like those of the maple, lack them altogether. In some leaves the stipules drop off shortly after the leaf matures. Stipules vary widely in shape and form. Ordinarily they are tiny leaf-like organs, but sometimes, as in the leaves of the garden pea, they are quite large and assist materially in photosynthesis. In the black locust and a few other plants, the stipules are thorns and in some species of *Smilax* they are tendrils.

Venation. The blade of the leaf is strengthened by the presence of veins. These veins are made up chiefly of vascular, or conducting, tissue which is continuous with that of the petiole. Hence, the veins serve to distribute water and dissolved inorganic salts throughout the different parts of the blade and to carry away elaborated foods as they are made.

There are two principal types of venation, or veining, *viz.*, **parallel venation** and **netted venation** (Fig. 18). In parallel-veined leaves, at least the principal veins all run parallel to each other from the base to the tip of the leaf or they may run parallel at right angles to a main central vein, as in the banana. This type of venation is characteristic of the monocotyledonous plants and is especially well exemplified in the grasses. In most leaves of this type there are tiny veins, invisible to the unaided eye, that connect the principal veins.

In netted-veined leaves the veins branch again and again, forming a complete network through the leaf (Fig. 18, D). The extreme tips of these branches usually end in the blade tissue. The nature of this type of venation can best be seen by holding a leaf like that of the maple, the catalpa, or the oak toward light. Netted venation is characteristic of dicotyledonous plants. In some netted-veined leaves, like those of the elm or the oak, there is a principal central vein, called the **midrib**, from which all other veins branch out. From its feather-like appearance, this type has been called **pinnate venation** (Fig. 18, B). In others, there are several large veins of equal size, all arising at a common point at the tip of the petiole and spreading out fan-like through the blade. This type of netted

venation is called **palmate venation** and occurs in leaves of mallow, geranium, maple, and many other plants (Fig. 18, *A*).

Simple and Compound Leaves. The blades of some leaves are deeply indented at the margins. Others are completely separated into individual parts called **leaflets** (Fig. 19). So long as the blade is in one piece, even though deeply lobed, the leaf is said to be **simple** (Fig. 17, II, *G-J*). When the blade is completely dissected into leaflets, the leaf is said to be **com-**

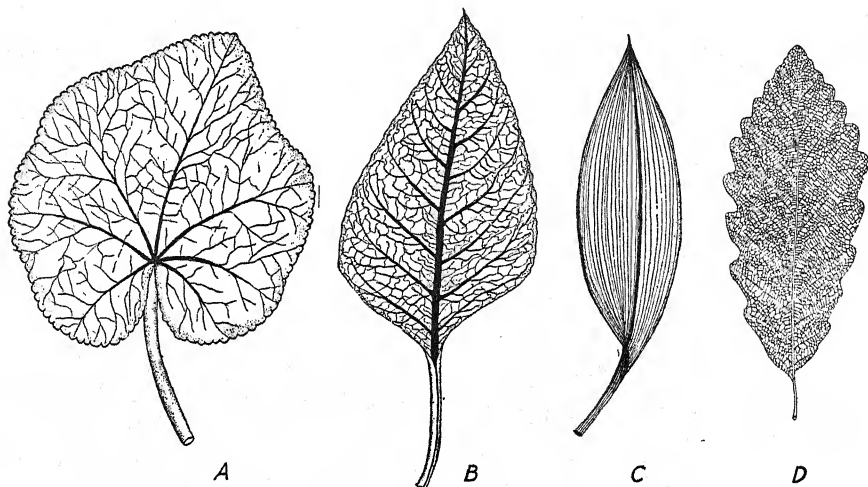


FIG. 18. Types of venation. *A* and *B*, netted venation; *C*, parallel venation. *A* show palmate type of netted venation and *B* shows pinnate type. *D*, leaf skeleton showing the connecting network of veins. (Drawings by Edna S. Fox.)

pound. There are two types of compound leaves: **palmately compound** leaves, in which the leaflets are all attached at a common point at the tip of the petiole (Fig. 19, *A*) as in clover and horse chestnut, and **pinnately compound** leaves (Fig. 19, *B*), in which there is a principal central axis, called the **rachis**, to which all the leaflets are attached. This type occurs in the rose and in the ash. The relation of these types of leaves to palmate and pinnate venation is obvious. The rachis of the pinnately compound leaf is homologous with the midrib of a pinnately veined leaf. The leaflets of a compound leaf may be either sessile or stalked and may have any of the types of margins characteristic of simple leaves. The leaflets may themselves be compound as in honey locust or in baneberry. In this case, the leaf is said to be twice or bipinnately compound. In a few cases, leaves are three times compound as in some of the acacias.

Pinnately compound leaves are sometimes mistaken for branches bearing simple leaves. The following features may be used to distinguish between them:

1. Leafy branches, especially of woody plants, often end in terminal buds; compound leaves never do.

2. Leaves usually have buds in their axils; leaflets ordinarily do not.
3. When stipules are present, they are usually found at the base of the whole leaf; not at the base of a leaflet.
4. When compound leaves of deciduous plants fall, the stem-like rachis also falls, although the leaflets may fall before the rachis does. Branches usually do not fall.
5. The leaflets of a compound leaf all originate and usually remain in a single plane, presenting collectively a flat surface comparable with the blade of a simple leaf. If the simple leaves of a leafy branch lie in the same plane, as they often do in horizontal branches with opposite leaves, it is because the petioles of alternate nodes have been

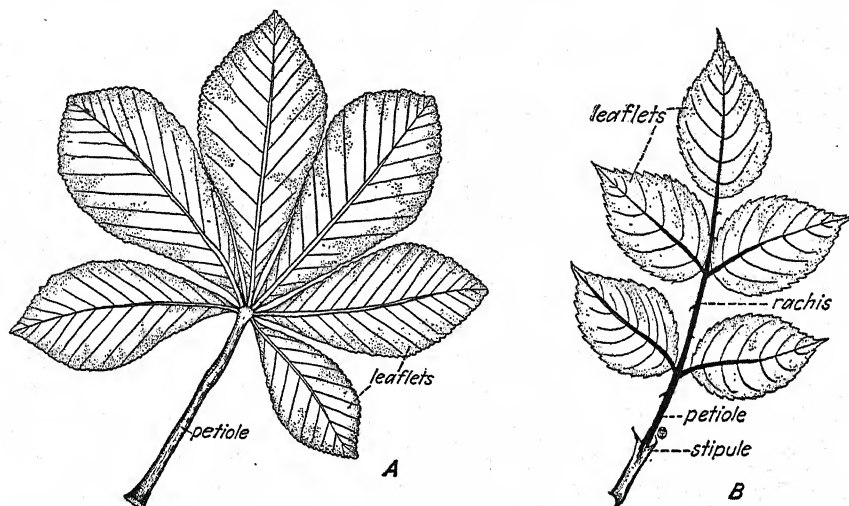


FIG. 19. Compound leaves. A, palmately compound; B, pinnately compound. (Drawings by Edna S. Foz.)

twisted around to bring the blades all into the same position. In other words, the leaves themselves originate in different planes.

Vernation. As before mentioned, leaves originate at the stem apex. Usually they are differentiated and grow much more rapidly than the stem tip itself elongates. Consequently, the leaves of several nodes may be found closely crowded together over the stem apex, forming a bud. As the stem elongates, the leaves become more widely separated, but before this happens they are usually folded, bent, or rolled up in the limited space they occupy. The manner in which the leaves are folded or rolled up in the bud is called **vernation**.

There are several distinct types of vernation, each characteristic of particular kinds of plants (Fig. 20). They are (1) *reclinate*, or *inflexed*, when the upper part of the leaf is bent down on the lower part as in the tulip tree; (2) *conduplicate*, when the leaf is folded lengthwise along the midrib, bringing the two halves of the blade face to face, usually with the lower surfaces outermost, as in the leaves of the cherry, the oak, and members of the magnolia family; (3) *plicate*, when the blade is folded back and forth along the main veins like a closed fan, as in palmately veined leaves like those of geranium, mallow, and maple; (4) *circinate*, when the leaf is rolled from the tip downward to

the base, as in ferns and in sundew; (5) *convolute*, when the leaf is rolled lengthwise from side to side, scroll-like, as in many members of the rose family and in lily of the valley; (6) *involute*, when both edges of the leaf are inrolled lengthwise on the upper surface toward the midrib, as in violets and water lilies; and (7) *revolute*, when both

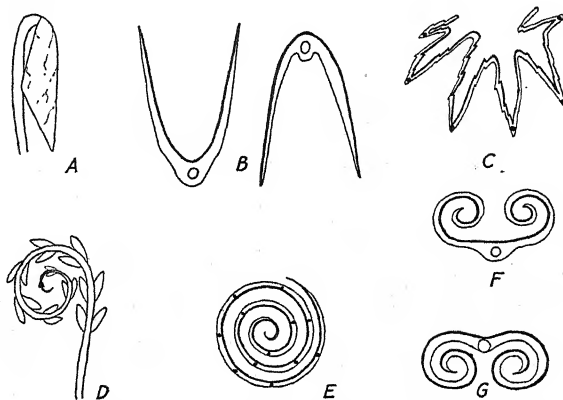


FIG. 20. Types of vernation illustrated diagrammatically. A, reclinate or inflexed; B, conduplicate; C, plicate; D, circinate; E, convolute; F, involute; G, revolute. (Drawn by F. Brown.)

edges of the leaf are inrolled lengthwise on the lower surface toward the midrib, as in azalea and dock.

Leaf Arrangement—Phyllotaxy. The actual positions occupied by leaves on the stem are determined (1) by inherent characteristics of the plant and (2) by environmental conditions. It is rather interesting that leaves are not haphazardly placed on

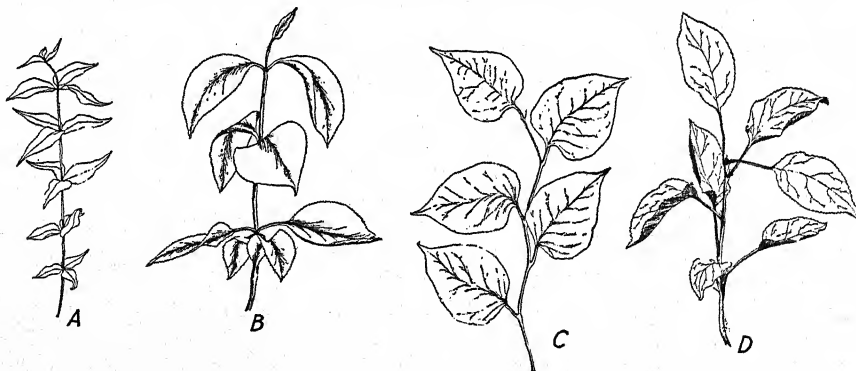


FIG. 21. Types of phyllotaxy. A, whorled; B, opposite; C, spiral, showing the one-half fractional arrangement; D, spiral, with the two-fifths arrangement. (Drawings by Elsie M. McDougale.)

the stem but arise with mathematical precision at definite and regular intervals. The arrangement of leaves on the stem is referred to as "phyllotaxy," a term meaning leaf order.

Leaves may be *opposite* (Fig. 21, *B*), in which case two leaves occur at a node, as in maple and mints; *whorled* (Fig. 21, *A*), when more than two leaves occur at a node, as in bedstraw, loosestrife, and some lilies; or *spiral* (Fig. 21, *C-D*), in which case only one leaf occurs at a node. When two leaves occur at a node, each pair usually stands at right angles to the next pair above or below, when the stem is in a vertical position, thus forming four rows or ranks around the stem as seen from above. This type of arrangement is also called *decussate* (Fig. 21, *B*). If the stem is horizontally placed, the petioles of the leaves of alternate nodes are usually bent around so as to bring the leaf blades into two horizontal rows or ranks.

In the simplest case of spiral phyllotaxy, every third leaf is directly over the first one of the cycle (Fig. 21, *C*), thus forming two vertical rows around the stem, as in elm and in corn and many other grasses. (This type is correctly referred to as *alternate*, but the term *alternate* has come to be used generally by botanists to refer to any spiral arrangement, *i.e.*, to any type in which there is only one leaf at a node.)

In the next type, every fourth leaf is over the first, forming three vertical rows, as in the beech, white hellebore, and the sedges. Perhaps the commonest spiral arrangement is the next type, in which every sixth leaf is directly over the first, forming five vertical rows or ranks. This is the type found in oaks, cherries, apples, and poplars. In the remaining types, the ninth, fourteenth, twenty-second, thirty-fifth, or fifty-sixth leaf, respectively, is over the first.

It is customary to designate spiral phyllotaxy by fractions representing the portion of the circumference of the stem between any two succeeding leaves in the spiral. These fractions may be determined by tying a string to the base of the petiole of any leaf and proceeding with

it, by the shortest route, to the base of the petiole of the next leaf, and so on, until a leaf is reached that arises directly over the first one. The numerator of the fraction would then be the number of complete turns made with the string around the stem, and the denominator the number of leaves touched, not including the first. In an apple twig, for example (Fig. 21, *D*), in which the sixth leaf is over the first, the string would pass twice around the stem and would touch five leaves, not counting the first, making the fraction $\frac{2}{5}$. The actual fractions found in this manner are $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, $\frac{8}{21}$, $\frac{13}{34}$, and $\frac{21}{55}$, the first three representing the first three types mentioned in the preceding paragraph. The higher fractions are usually found in plants with greatly shortened stems, like the common rosette plants, and in pine cones. The arrangement of leaves on a stem usually falls into one or another of these fractions. There are seldom any intermediates or variations from them, except that stems are sometimes twisted enough to obscure the actual type of phyllotaxy. Even in this case, the change will usually be to another of the fractions already mentioned. It is also interesting to note, on examining these fractions, that in all cases

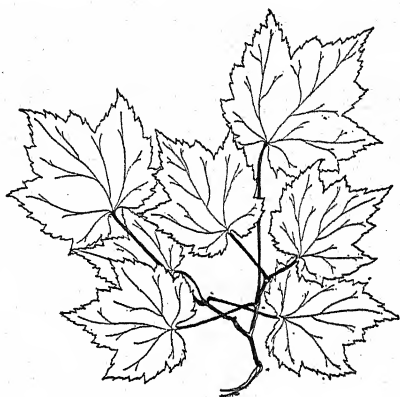


FIG. 22. Leaf mosaic of maple showing variations in lengths of petioles which result in the orientation of the leaf blades more or less in a single plane facing the direction of the incident light. (Drawing by Elsie M. McDougle.)

after the first two the numerators and denominators are each the sum of the two preceding and that the numerators are the same as the denominators of the second preceding fractions. The denominators also represent the number of rows or ranks of leaves one would see on looking vertically down on the stem producing them.

Phyllotaxy deals only with the arrangement of leaves as determined by their points of origin on the stem. The actual arrangement of the leaves is greatly influenced by the position with respect to light of the leaf, the stem, or the plant as a whole. Leaves are usually found in positions that enable them to receive a maximum amount of the incident light. Thus, on vertical stems, and especially in rosette plants, the petioles of the leaves are usually increasingly longer from the tip to the base of the

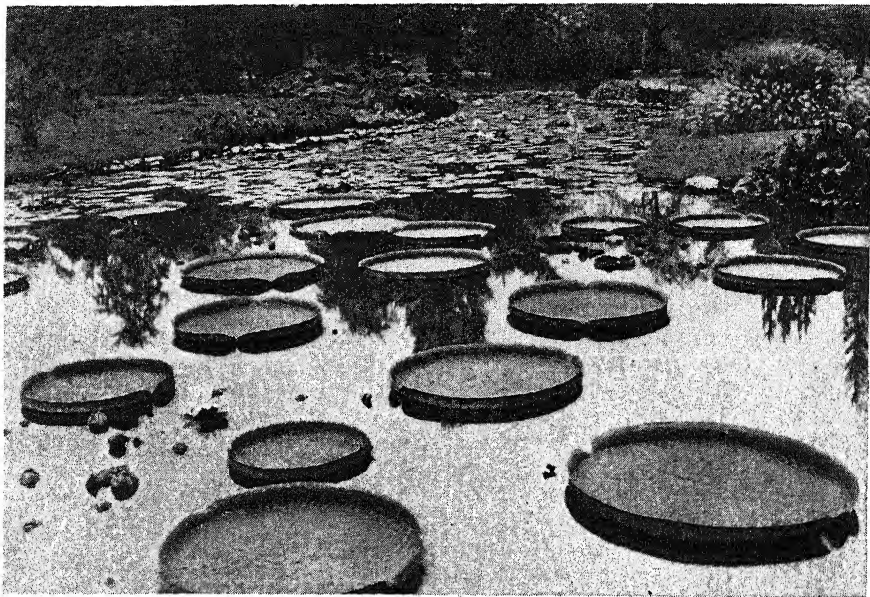


FIG. 23. Floating leaves of water lilies (*Victoria regia*). (Photograph by Dr. Paul Shope; taken at Tower Grove Park, St. Louis, Mo.)

stem. One-sided illumination may cause the true arrangement of the leaves to be obscured, as in a leafy vine growing on a brick wall. In this case, the leaves are all directed outward, forming a mosaic (Fig. 22). In the compass plant (*Silphium laciniatum*) and in wild lettuce (*Lactuca scariola*) the leaves all face east or west regardless of their phyllotaxy. The crowding of plants in dense colonies also greatly affects the arrangement of their leaves. Sometimes the leaves of such plants are long and narrow and are placed in a position parallel to the rays of the sun. This is the situation with many reeds and sedges and in cattail colonies. Such arrangements cut down shading to a minimum.

Other arrangements result from the water relations of the plant. In the water lilies, the leaves float on the surface of the water, apparently without any definite arrangement, the rest of the plant being submerged, with the roots in the soil, under the water (Fig. 23).

ANATOMY OF THE LEAF

The internal arrangement of the tissues of the leaf can be understood best by a microscopic examination of very thin slices or cross sections cut at right angles to the broad surface of the blade. Sections cut in this manner will show several well-defined regions in the leaf blade (Fig. 24). The outermost layer of cells, which extends all over the surface of the leaf, is called the **epidermis**. The interior of the leaf, between the upper epidermis and the lower epidermis, is called the **mesophyll**, a term meaning

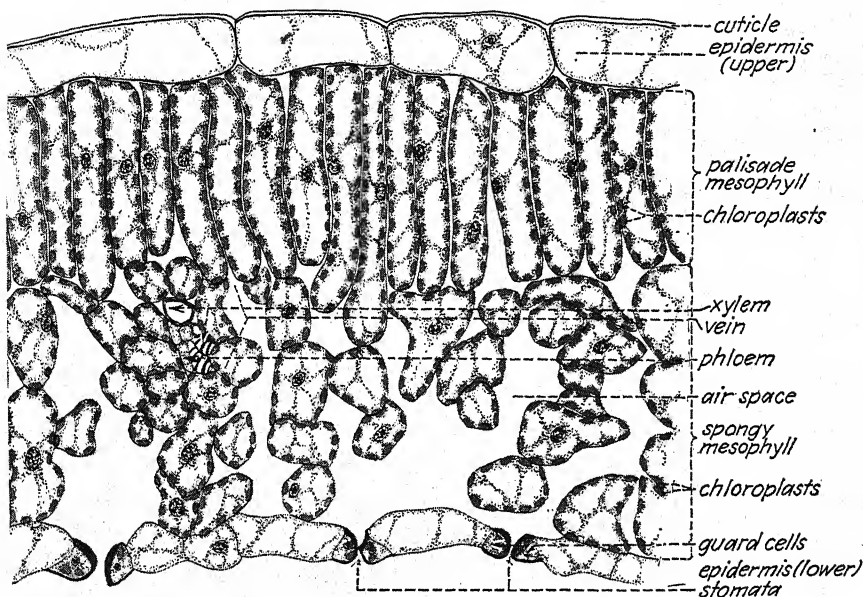


FIG. 24. Cross section of a portion of a leaf of *Lonicera tatarica* showing structure. (Drawing by Helen D. Hill from slide furnished by J. W. Sinden.)

“middle of the leaf.” The mesophyll is further differentiated into an upper region, the **palisade mesophyll**, and a lower region, the **spongy mesophyll**. The **veins**, or **vascular tissues**, extend throughout the spongy mesophyll. The outstanding characteristics of these tissues are considered separately.

The Epidermis. The epidermis usually consists of a single layer of cells that appear more or less rectangular in shape as seen in cross section (Fig. 24). In surface view, they are often very irregular in shape. On the upper surface of the leaf, the exterior or upper walls of the epidermal cells are thickened by a special colorless layer known as the **cuticle** (Fig. 24). This cuticle is made up of a waxy, waterproof mate-

rial, called cutin, which prevents the drying out of the underlying tissues and protects them to some extent against mechanical and other injuries. The mature cells of the epidermis are usually colorless throughout and contain a comparatively small amount of protoplasm lying against the cell walls and a large central vacuole filled with cell sap. In some seed plants, the cell sap of the epidermal cells may be colored with anthocyanin, but chlorophyll is never found except in a few submersed plants. Depending upon the species and upon the environmental conditions under which a plant grows, there may be one or several layers of epidermal cells. The epidermis is more likely to consist of several layers in plants growing under intense sunlight and in dry situations. The epidermal cells of submersed plants and of those growing in moist places are usually larger than those of plants growing in dry habitats. The epidermis of the lower surface of the leaf usually consists of a single layer of cells, similar in structure to those of the upper surface but less regular, and with thinner outer cell walls, covered with less cutin.

Epidermal Hairs. As previously stated, the outer surface of the epidermis consists of a cuticle. In addition to this cuticle there may be other waxy or resinous coverings, sometimes forming a "bloom" over the leaf surface. In many plants the epidermis is covered with various kinds of hairs (Fig. 25). These hairs may be restricted to the lower or to the upper epidermis or may occur on both upper and lower surfaces. They may be simple, unicellular epidermal outgrowths or complex, multicellular structures. They are often much branched. Sometimes they consist of living cells. Many of these are glandular, secreting oils and other substances. The stinging hairs of nettle come under this category. They are elongated, tapering, unicellular structures, containing a fluid which is held under considerable turgor pressure. The tips of these hairs are enlarged somewhat and are turned slightly to one side. When touched, the end usually breaks off, leaving a point like a hypodermic needle. This easily pierces the skin and injects the fluid, which causes considerable irritation.

The hairs of other plants are dead in the mature leaf and often filled with air. In the common mullein (*Verbascum thapsus*) these dead hairs are branched (Fig. 25, C) and are produced in such profusion as to give the leaf a woolly or felt-like appearance. In many members of the mustard and mallow families the hairs are star-shaped (stellate). In other plants they may be scale-like. Sometimes they are soft, filamentous structures giving the leaf a velvety appearance, while at other times they are stiff and hard, like the leaf spines of thistles.

While most of the different types of epidermal hairs are characteristic of particular species of plants, their development is greatly influenced,

at least in some plants, by environmental conditions. The production of leaf hairs is usually most pronounced in plants living under dry conditions. Young leaves are usually more densely covered with hair than older leaves. This is especially true of many perennial plants with resting buds that open during cool weather in the spring. The young leaves in the buds of horse chestnut are so hairy as to be hardly recognizable as leaves; but

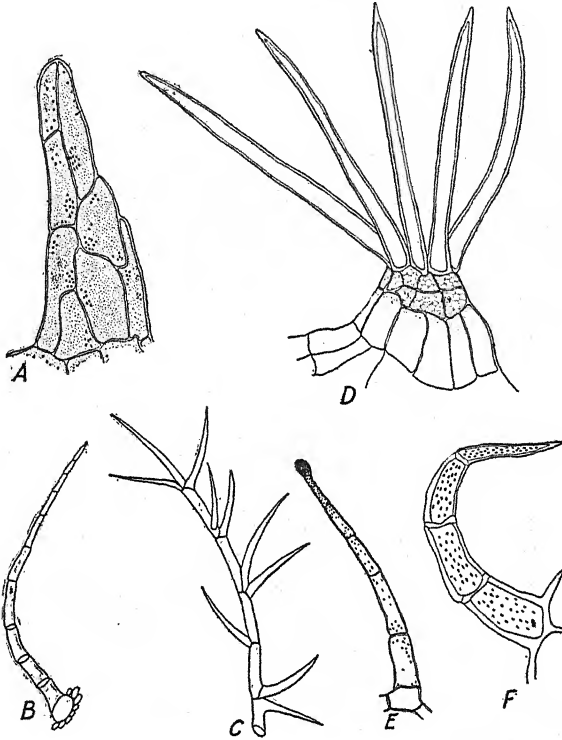


FIG. 25. Types of epidermal hairs. A, *Begonia*; B, *Coleus*; C, *Verbascum*; D, *Malva*; E, *Petunia*; F, *Pleroma*. (A, B, D, and F drawn by L. J. McConnel and Chris. Hildebrandt.)

as the leaves emerge from the bud and expand, this hairiness gradually disappears.

Stomata. The lower epidermis, and sometimes the upper, is perforated by numerous pores known as stomata (singular, stoma) (Figs. 24, 26). Each stoma is a minute opening between two highly specialized epidermal cells called **guard cells**. While the term stoma is applied, strictly, only to the opening between the guard cells, it is sometimes used also to refer to the whole structure comprising the guard cells.

Stomata can best be observed by examining the epidermis in surface

view. The lower epidermis of many leaves can be peeled off readily, especially after the leaf has been rubbed for a while between the fingers and thumb. When a section of the epidermis, peeled off in this manner, is examined under a microscope, the stomata stand out in striking con-

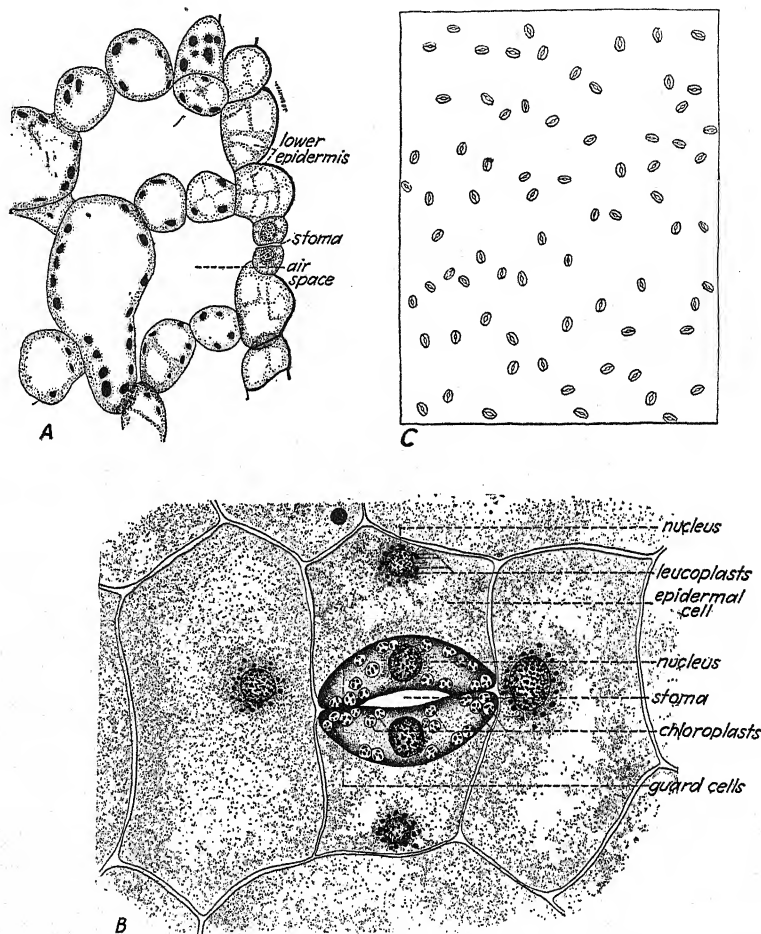


FIG. 26. *A*, cross section of a portion of barberry leaf showing a stoma in communication with an air space; *B*, surface view of a stoma from leaf of *Tradescantia*; *C*, diagram illustrating distribution of stomata on geranium leaf; dimensions of the section, $576 \times 800 \mu$, or about 0.46 sq. mm. (*A*, drawn by J. G. Bechtel; *B*, by Elsie M. McDougale.)

trast to the rest of the epidermis. The two guard cells appear bean- or crescent-shaped and are attached to each other by the curved ends of their concave sides, leaving a slit-like opening, the stoma proper, between them and presenting together a circular or oval form (Fig. 26, *B*). In its most

expanded condition, the opening between the guard cells is considerably smaller than a pinhole. The smallest visible hole that one could make with an ordinary laboratory dissecting needle in a sheet of paper of the thickness of this page would be about $100\ \mu$ ($1\ \mu = 0.001\ \text{mm.}$). In comparison with this, the average stoma is only about $18\ \mu$ long and $6\ \mu$ wide. By actual measurement, the average area of the opening in 37 kinds of cultivated plants has been found to be $92\ \text{sq.}\ \mu$.

The walls of the guard cells that border on the stoma are usually thicker than the outer walls (Fig. 24). The protoplasm is usually denser than that of the ordinary epidermal cells, and there is always present a rather conspicuous nucleus. Starch is usually found in the protoplasm of guard cells even though it may not normally be present in the other cells of the leaf, as is the case in many monocotyledonous plants. Unlike the ordinary epidermal cells, the guard cells contain chloroplasts and hence appear green. The significance of these chloroplasts and of the general structure of the guard cells will appear presently.

Opening and Closing of Stomata. The stomata are not merely pores in the epidermis but pores capable of being opened and closed. It has already been mentioned in connection with guard cells that the walls that border on the stoma proper are usually thicker than the outer walls. This unequal thickness of the opposite walls, together with the shape of the guard cells and their position with respect to each other, is responsible for the fact that when the guard cells are turgid, *i.e.*, bulged out by the internal pressure of their liquid content, the opening between them is greatest or, in other words, the stoma is wide open. When the guard cells are limp (flaccid), the stoma is closed. The opening and closing of the stomata are thus governed by changes in the turgor of the guard cells.

Two kinds of explanations have been advanced to account for the turgor changes in the guard cells. One of these deals with carbohydrate transformations in the guard cells and the other with colloidal hydration (swelling of the colloids by imbibing water) and dehydration. In both explanations, light and the acidity of the guard cells are considered important factors.

The first and the older of the two theories explains the changes in turgor in terms of transformations of starch to sugar and sugar to starch. It has previously been stated that the guard cells alone of the epidermal cells contain chlorophyll. They are therefore able to manufacture carbohydrates in light. The guard cells usually contain starch. The stomata of many plants are closed at night. In the morning, when light falls on the guard cells, some of the starch they contain is changed to sugar and probably more sugar is manufactured by the chloroplasts they contain. This sugar, being soluble in the water content of the cell, renders the solutions in the guard cells more concentrated and osmotically active, *i.e.*, enables them to draw water from the surrounding epidermal cells, the concentration of which is relatively less. As this water is absorbed, the guard cells swell and become turgid, which causes the stomata to open. At night, in the absence of the controlling factor light, the sugar of the

guard cells is changed back to starch; and since starch is insoluble in water, the concentration of dissolved material in the guard cells is reduced to such an extent that adjacent epidermal cells become relatively more concentrated and thus are able to draw water from the guard cells. This causes the latter to shrink again and closes the stomata. The transformation of starch to sugar takes place best when the cell sap is less acid, and the reverse transformation when the cell sap is somewhat more acid. The guard cells, like all living cells, carry on respiration and in so doing give off carbon dioxide, which combines with water to form carbonic acid. In the daytime, this carbonic acid is consumed in photosynthesis and leaves the cell content neutral or less acid. At night, on the other hand, the carbon dioxide accumulates, since photosynthesis does not take place, and causes the cell content to become weakly acid. These normal changes in acidity support the theory of carbohydrate transformations as causing the opening and closing of the stomata.

The colloidal hypothesis differs from the foregoing explanation chiefly in assuming that the changes in acidity of the cell content, resulting from the effect of light on the guard cells, causes the colloids normally present in the guard cells to swell, altogether aside from the effect it may have on the carbohydrates. It is the swelling of these colloids which is then thought, according to this hypothesis, to cause the guard cells to bulge out and to open the stomata. The increased acidity at night is thought to cause the colloids to shrink again and to close the stomata. The details of the colloidal hypothesis are too intricate to be considered further here. It is possible that both explanations are correct. Since the stomata of different plants do not all operate in the same way, it is possible that one explanation fits one kind of stoma and another another, but it is not impossible that both methods could operate in the same guard cells.

The opening and closing of the stomata regulate the exchange of gases between the interior tissues of the leaf and the surrounding atmosphere, this exchange being necessary for respiration and for photosynthesis. Under these conditions, the escape of water vapor also takes place, even though it may prove detrimental to the plant. It is important to note that the plant is wholly incapable of closing its stomata in anticipation of wilting. The opening and closing of stomata are entirely chemical and physical processes to which the plant is entirely passive. The diffusion of gases and water vapor through the stomata is further facilitated by the invariable presence of an air chamber in the spongy mesophyll immediately beyond the stoma and communicating with it.

In most thin-leaved dicotyledonous plants of humid regions, the stomata are open all day and closed all night. In the potato, the stomata are open continuously except for about 3 hr. following sundown. The stomata of cabbage, pumpkin, squash, tulip, and onion also tend to remain open continuously. The stomata of cereals like wheat, oats, and barley are closed all night and only partially open during the day.

Distribution of Stomata. In many leaves the stomata are confined to the lower surface. In others they occur on both surfaces and in the floating leaves of water plants they may be present only on the upper surface. In number, they average around 100 to 300 per square millimeter of leaf

surface (Fig. 26, C), but as many as 1,400 per square millimeter have been found in mature leaves of oak. When it is realized that a square millimeter is an extremely small area, slightly less than the area of the end of the lead in a lead pencil, it becomes obvious that stomata are numerous. The actual numbers of stomata found in the leaves of some common plants are given in the table shown below.

AVERAGE NUMBER OF STOMATA PER SQUARE MILLIMETER OF LEAF SURFACE

Plant	Upper surface	Lower surface
Common pea.....	101	216
White water lily.....	460	0
Olive.....	0	625
Sunflower.....	175	325
Norway maple.....	0	400
Black walnut.....	0	461
Tiger lily.....	62	62
White pine.....	142	0
Pumpkin.....	28	269
Wheat.....	33	14

It should perhaps be mentioned that stomata are not confined to leaves but occur on all parts of the plant that have a functioning epidermis, except roots.

The Mesophyll. Between the upper and the lower epidermal layers is the important region of the leaf known as the mesophyll. The cells lying next to the upper epidermis are roughly rectangular in shape as seen in the cross section of the leaf, with the long axes of the cells at right angles to the surface of the leaf. These cells are arranged, palisade-like, in one or more rather compact layers or rows, from which fact they have received the name **palisade mesophyll** (Fig. 24). What air spaces there are between these cells are usually very small. The cells are filled with chloroplasts, which gives the upper surface of the leaf a much darker green color than the lower.

The cells of the lower part of the mesophyll are very irregular in shape and much less compact. There are large and numerous intercellular spaces extending throughout this region, giving it a rather spongy appearance. Hence, it has been called the **spongy mesophyll** (Fig. 24). The intercellular spaces of the spongy mesophyll are in direct communication with the stomata of the lower leaf surface and hence with the surrounding air. By this means almost every cell of the mesophyll can receive carbon dioxide and oxygen directly from the atmosphere or pass off these gases to the atmosphere. The cells of the spongy mesophyll also contain chloro-

plasts, but these are seldom as numerous as they are in the palisade mesophyll.

All the ordinary cells of the mesophyll belong to the type of tissue known as parenchyma. Since the cells of the mesophyll also contain chloroplasts, they are sometimes called **chlorenchyma**. The chlorenchyma cells of the mesophyll are the chief carbohydrate manufacturing cells of the plant.

The description thus far given for the mesophyll applies chiefly to ordinary dicotyledonous plants. Even in these, the structure is sometimes quite different from the one described. Some of these differences

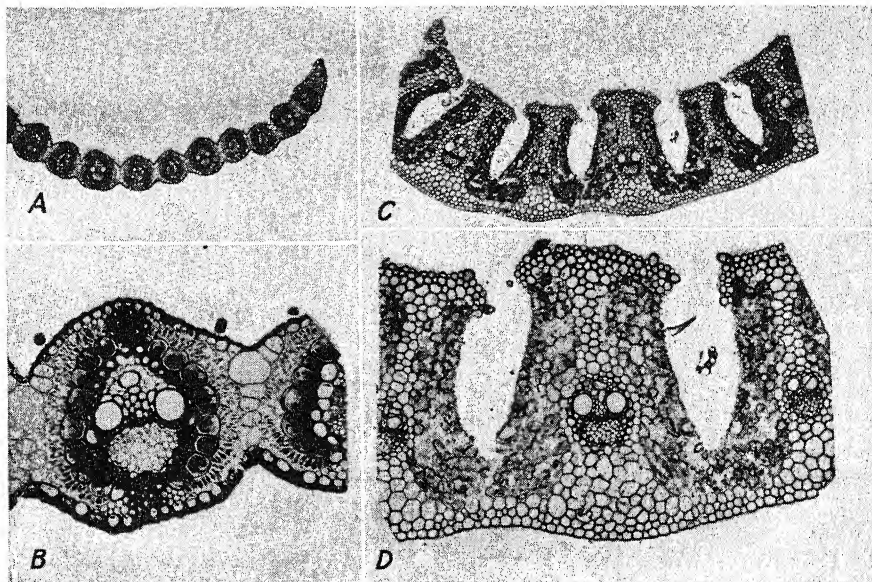


FIG. 27. Leaves of monocotyledonous plants in cross section; *B* and *D* more highly magnified views of *A* and *C*, respectively; *A* and *B*, a xerophytic grass leaf; *C* and *D*, *Ammophila*.

are characteristic of particular species of plants, and others are caused by the environment in which the plant grows. In general, the mesophyll tissues are much more compact, with fewer air spaces, when plants are grown in direct sunlight. Under these conditions there may be two or three palisade layers. In the shade, on the other hand, the palisade mesophyll may appear more like the spongy mesophyll. The monocotyledonous plants as a whole, and the grasses in particular, often present an entirely different appearance in cross section (Fig. 27). In the grasses there is no well-defined differentiation of the mesophyll into palisade and spongy tissue. The cells are more or less compact and angular throughout, with air spaces occurring only next to the stomata, but these occur on both

the upper and the lower surfaces of the leaves. Many other variations occur.

The Veins. Standing out rather conspicuously in the spongy mesophyll tissue, as seen in cross section, are the veins of the leaf (Fig. 24). The veins are the terminals of a vascular system which extends throughout the plant from root to leaf and functions in the conduction of water, minerals, and organic substances and in strengthening and support. The veins, or vascular bundles, of the leaf blade are, in general, restricted to the spongy mesophyll, but the largest ones, like the midribs, may extend from the upper to the lower epidermis. In netted-veined leaves, the veins branch again and again and in all directions. Consequently, in a cross section of such a leaf, some of the veins will be cut lengthwise and others crosswise, with all gradations between. Since the veins become progressively smaller as they branch out in the mesophyll tissue, the size of the different sections will also vary. Cross sections of leaves of grasses, in which the veins are parallel, will show only cross sections of the veins.

The largest veins usually consist of three distinct tissues, an outer **sclerenchyma sheath**, a group of water-conducting cells, called **xylem**, lying toward the upper surface of the leaf; and **phloem**, or food-conducting tissue, lying toward the lower surface (Fig. 28, A-C).

The **sclerenchyma sheath** consists of rather thick-walled, fibrous cells that give strength to the vascular bundle. This sheath may completely surround the bundle or it may be restricted to the upper and lower sides of the bundle. It is only the main veins that have a sclerenchyma sheath. In the smaller veins, the sheath consists of colorless parenchyma cells usually referred to as **border parenchyma** (Fig. 28, B).

The **xylem** of the vein consists of elongated cells with internal, often spiral or reticulate, thickening (Fig. 28, C). These are the principal water-conducting cells and have much the same structure as they do in other parts of the plant. The individual cells are joined end to end, to form long tubes called tracheae or vessels. The xylem of the main veins also consists of fibers and parenchyma cells. As the veins become smaller by branching, the size of the xylem decreases. Finally, a single vessel, or tracheid, may be found ending in the mesophyll tissue.

The **phloem** of the bundle, like that found in other parts of the plant, usually consists of sieve tubes, companion cells, and ordinary parenchyma cells. The characteristics of these cells have been described in a previous chapter. It is the sieve tubes that transport the foods out of the leaf as they are manufactured. As the veins become progressively smaller, the phloem tissues are reduced so as to consist ultimately of only parenchyma cells.

The veins are so thoroughly distributed throughout the spongy mesophyll

tissue that any one manufacturing cell is, at most, only a few cells away from its water supply and is also in more or less direct communication with the phloem.

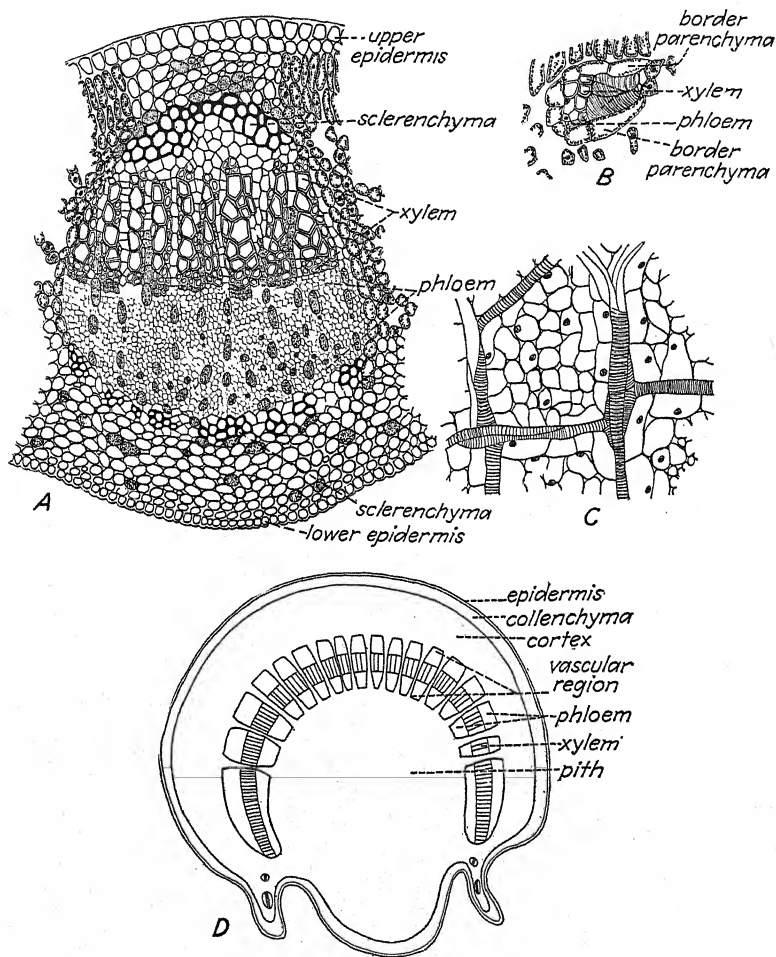


FIG. 28. A, cross section through one of the larger veins of a leaf of pear; B, cross section through a smaller vein of the same leaf; C, section through a leaf of tobacco cut parallel to the surface, showing veins in lengthwise view; D, diagram of cross section through a petiole of a potato leaf. (Drawings by Helen D. Hill.)

The Petiole. The internal structure of the petiole appears, in cross section, more like that of a young stem (Fig. 28, D). There is an epidermis around the outer portion and a large mass of fundamental or parenchyma tissue within, traversed by one or more strands of vascular tissue. Usually there are several separate vascular bundles arranged in

a circle or in a semicircle as seen in cross section. These bundles consist of a sclerenchyma sheath, xylem, and phloem. The xylem is situated toward the upper side of the petiole and the phloem toward the lower side. The vascular bundles are continuous with those of the stem and also join those of the leaf. Often there are groups of sclerenchyma cells just inside the epidermis. These, together with the sclerenchyma around the bundles, serve to strengthen the petiole.

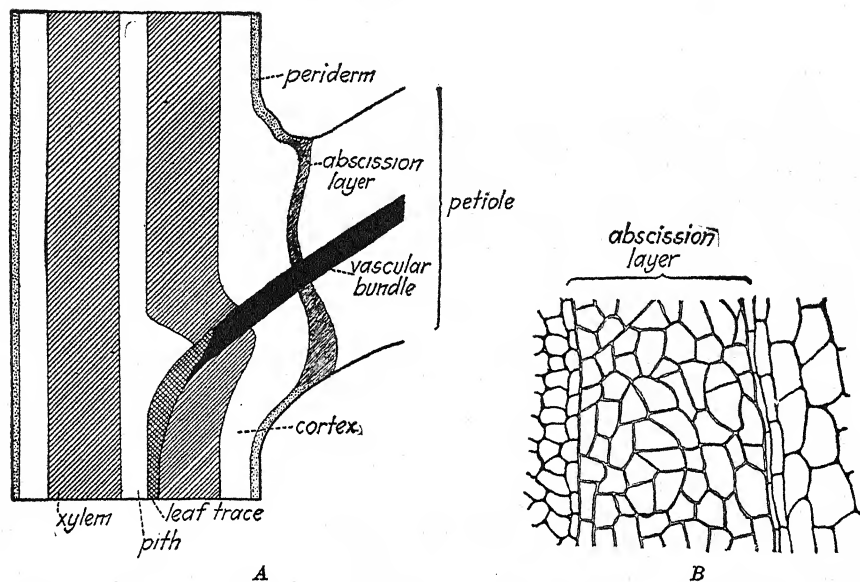


FIG. 29. A, diagram to show leaf abscission layer; radial section through twig and leaf base in *Juglans cinerea*. The abscission layer extends through the vascular bundle only in parenchyma cells; all other cells are broken mechanically. B, detail of cellular structure of a small part of the layer three weeks before leaf fall. (From A. J. Eames and L. H. McDaniels, "Introduction to Plant Anatomy," McGraw-Hill Book Company, Inc., New York, 1925.)

Abscission and Leaf Fall. In temperate regions, the leaves of plants sooner or later cease functioning and die. In some plants, the dead leaves remain on the plant until they decay and disintegrate, but in many woody plants, like the common broad-leaved trees, all the leaves are regularly shed in autumn. This is brought about by the development, at the base of the petiole where it is attached to the stem, of a special layer of cells called the **abscission layer** (Fig. 29). This layer usually starts to develop long before the leaves actually fall. It consists of a band of parenchyma cells extending all through the basal region of the petiole except through the vascular tissues. As the season progresses, the walls of the cells of the abscission layer become softened and gelatinous by chemical action. This causes them to separate from one another until finally the leaf is held only

by the vascular tissue. Sooner or later, the vascular tissue also becomes ruptured by the swaying of the leaf in the wind or by the action of frost, and the leaf falls. The action of frost in this connection may be observed on bright, sunny mornings following cold, frosty nights. As the sun melts the ice formed where the abscission takes place, the leaves often fall in showers. In some oaks and in other plants it is not uncommon to find some of the dead leaves remaining on the tree over winter. This may be caused by the failure of the vascular strands to break or by the failure of the abscission layer to develop fully.

Along with the abscission layer there is usually developed, between it and the stem, a protective layer consisting of corky (lignosuberized) cells. This layer may develop before the leaf falls or later. In some cases, it is formed by transformations in the walls of cells already present and in others by cell division, giving rise to a corky tissue similar to that found in the outer portion of the stem. In any case, this corky layer tends to heal over the scar left by the falling leaf.

Plants that regularly shed all their leaves at the end of the growing season are known as deciduous plants. Those that retain them throughout the year are known as evergreen plants. The leaves of such evergreens as the rhododendrons, some laurels, pines, spruces, and most other conifers often persist from 3 to 4 years or more. Even in these plants there is a more or less periodic fall of the older leaves. The white pine, for example, sheds rather abundantly in late autumn, but the leaves shed are usually those which were produced the second or third year preceding.

PHYSIOLOGICAL PROCESSES OF LEAVES

Certain physiological processes are common to all living cells wherever they occur in the plant. Among these may be mentioned digestion, respiration, and assimilation. Since the leaf consists almost entirely of living cells, it carries on all these processes. Because of its particular structure and position, however, the ordinary leaf carries out certain physiological processes more intensively than others. Most prominent among these are photosynthesis, or the manufacture of carbohydrates, and transpiration, which is the giving off of water vapor by the plant. Photosynthesis is taken up in the following chapter. It may be emphasized here, however, that the leaf is the outstanding center of this important process in the plant. In the present chapter only transpiration is considered.

TRANSPIRATION

Transpiration may be defined as the giving off of water vapor from the internal tissues of living plants. This type of water loss is common

to all terrestrial plants. It may take place from any exposed part of the plant, but the structure and the position of the leaves are such that the greatest loss of water usually occurs through them. That such loss actually occurs can be readily demonstrated by placing a potted plant under a dry bell jar. Even when the soil is sealed off with paraffin, so that no water can escape except through the plant, moisture will soon collect on the sides of the bell jar as the inside air becomes saturated and will ultimately run down the walls in rivulets. A bell jar without a plant will not collect condensed moisture in this manner under the same conditions.

The actual amount of water lost by transpiration can be determined quantitatively by weighing at regular intervals a potted plant, the soil of which has been sealed over with paraffin or rubber dam in such a manner that no water can escape except from the plant. When this is done, it will be found that the plant continues to lose weight. It can easily be proved that this loss in weight is almost entirely caused by transpiration. A striking visual method of determining the rate of transpiration is by means of a potometer (Fig. 30) in which the loss of water causes a bubble of air to move across a scale.

Cuticular and Stomatal Transpiration. Two types of transpiration are recognized, *viz.*, cuticular transpiration, or the diffusion of water vapor directly through the cuticle of the epidermis, and stomatal transpiration, which takes place through the stomata. The former is usually of less importance, being responsible for less than 10 per cent of the total amount of transpiration from leaves under ordinary conditions.

By far the greatest loss of water from the plant takes place through the stomata of the leaves. The structure and mode of operation of the stomata have already been considered. It was stated that the opening of the stomata is necessary for the exchange of gases in photosynthesis and that, when they are open, water is unavoidably lost through them. The loss of water may be so great that transpiration exceeds the rate of water absorption and hence results in wilting. It is for this reason that the broad leaves of plants like the common pumpkin sometimes wilt partially on a hot, sunny day. The plant has no power to stop this loss. Only after wilting has begun do the stomata close, and then only because the guard cells, along with the other leaf cells, have lost their turgidity.

Relation to Evaporation. Transpiration might also be defined as evaporation from living plant tissues. One essential part of the process is the same as in evaporation, *viz.*, the transformation of water into water vapor. The same factors that influence the rate of evaporation from a nonliving surface have similar effects on transpiration. The difference is that transpiration takes place from living tissues and is therefore influenced by the

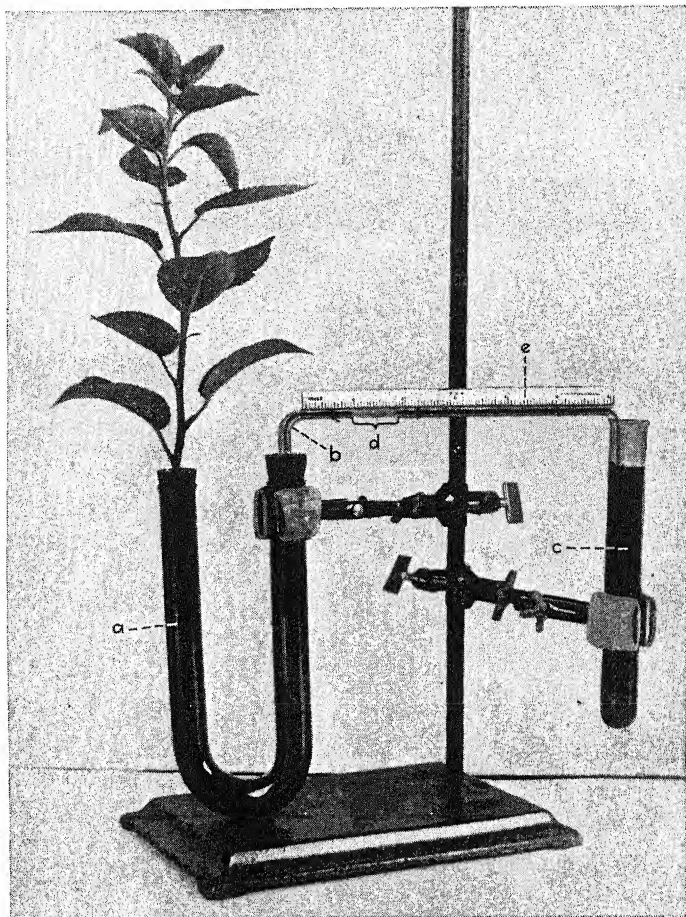


FIG. 30. Potometer for studying rate of transpiration. A leafy twig is fastened by means of a perforated and cut rubber stopper into one arm of a U-tube, *a*, filled with boiled and cooled water to which a little thionin has been added. A bent capillary tube, *b*, is forced down into the other arm of the U-tube until the liquid has been forced out of the free end of the capillary. As water is lost by transpiration from the leafy shoot, air is drawn into the free end of the capillary. As soon as a bubble of air has been drawn into the tube, the free end is lowered into a test tube, *c*, also filled with boiled water colored with thionin. The rate of transpiration is determined by noting the time required for the bubble, *d*, to move across the scale, *e*, fastened to the back of the capillary tube. To force the bubble back to the zero mark of the scale, the capillary tube is pushed down lower into the U-tube. The comparative influence of light, darkness, air currents, and various temperatures can be determined by this method.

structure and physiology of the plant, while evaporation is controlled entirely by environmental factors. It is for this reason that transpiration is considered to be a physiological process.

When considered on the basis of leaf area involved, transpiration is always considerably less than evaporation from an equal area. Thus it has been

found that under the same conditions the rate of transpiration from a sunflower plant at night is only about one-fourth the rate of evaporation from a free surface of water and during the day about three-fourths. These values vary considerably with different plants.

Conditions Affecting the Rate of Transpiration. The rate at which a plant gives off water vapor is not constant but fluctuates with the condition of the surrounding atmosphere as well as with a number of conditions operating within the plant itself. These two types of conditions may be referred to as external factors and internal or plant factors, respectively.

External Factors. The most important of the external factors affecting the rate of transpiration are radiant energy, humidity, temperature, air currents, atmospheric pressure, soil factors, and films of dust and other materials on leaves.

Radiant Energy. The source of radiation for plants growing out of doors consists of direct and reflected radiation from the sun. This radiation consists not only of visible rays, or light, but also of invisible ultraviolet and infrared rays. It is the visible radiation, or light, that causes the stomata to open, thereby exposing the saturated interior cells of the leaf to the atmosphere and greatly increasing the rate of transpiration. But, in addition to this, transpiration is still further increased because many of the cell constituents absorb radiant energy and transform it into heat, which is effective in increasing the vaporization of water. Such absorption is not restricted to visible radiation but takes place also in the ultraviolet and especially in the infrared. Of the total radiant energy that falls on a leaf, about 10 per cent is reflected, 10 per cent is transmitted through the leaf, and about 80 per cent is absorbed. Some of the absorbed energy is used in photosynthesis and perhaps in other ways, and some is reradiated from the leaf, but a large amount is dissipated in transpiration. It is for this reason that the rate of transpiration is closely correlated with changes in intensity of the incident radiation. Since the intensity of daylight gradually increases from morning to noon and falls again from noon to night, we should expect a corresponding increase in transpiration rate from morning to noon and a decrease from noon to night. Such is actually found to be the case. The maximum rate, however, usually occurs between 1:00 and 2:00 P.M. and the minimum rate at night. Transpiration is never so rapid at night as it is on a bright, sunny day. In the cereals, the average rate of transpiration at night has been found to be only 3 to 5 per cent of the day rate, and in many plants the rate is at least five times as great during the day. The wide variations in intensity of the sun's radiation with cloudiness, altitude, latitude, and season cause corresponding changes in the rate of transpiration. The combined effect of radiation in causing the stomata to open and in increasing the vaporization of water makes it the most important single external factor affecting transpiration.

Humidity. The amount of water vapor in the atmosphere immediately surrounding the plant is also an important factor influencing water loss. Transpiration is to be regarded as a diffusion process in which water vapor passes from a region of high concentration (the intercellular spaces of the leaf) to a region of lower concentration (the outside air). The rate of such diffusion depends directly upon the relative concentrations of the diffusing material. The air in the intercellular spaces of the leaf is usually near the saturation point. If the external atmosphere is nearly or quite saturated, as on damp, foggy days, little transpiration will occur. In general, the rate of transpiration varies inversely as the humidity of the atmosphere, the effect of humidity in this case being the same as it is with evaporation. It has been found, however, that some transpiration still occurs even in a saturated atmosphere. This is probably because the internal temperature of the leaf may be a few degrees higher than that of the surrounding atmosphere.

Temperature. The effect of increased temperature is to increase transpiration, not only because it hastens the purely physical process of transforming water into water vapor but also because air at a high temperature is capable of holding more moisture than cold air. When the temperature of the atmosphere is increased, therefore, its water-holding capacity is increased and thus transpiration increases. Low temperatures, conversely, lower the amount of transpiration, other factors being constant. It is thus obvious that temperature effects are closely correlated with effects of humidity. The importance of radiant energy in tending to increase the internal temperature of the leaf has already been mentioned. Plants, unlike higher animals, do not maintain a constant temperature but tend to acquire the temperature of their surroundings. Any increase in the temperature of the atmosphere, therefore, tends to increase the temperature of the plant and hence increases the rate of transpiration.

Air Currents. Air currents have the same significance in transpiration as in evaporation from a free water surface. When the air immediately surrounding the transpiring surface is being constantly renewed by air currents, transpiration will be increased. If not so removed, this air becomes more saturated with water vapor, the difference in humidity between the external and the internal air becomes less, and transpiration is lessened. It has been found, however, that moderate air currents are more effective than a strong wind.

Atmospheric Pressure. The barometric pressure of the atmosphere affects the rate of transpiration because it influences the rate of vaporization of water. For this reason, evaporation of water is more rapid in a vacuum than it is in air. In general, the higher the pressure the lower will be the rate of transpiration. This factor is of minor importance in any

given locality but is quite effective in a comparison of transpiration rate at high altitudes with the rate at low altitudes. In high altitudes the pressure is low. Since there is likely to be also a low humidity and a high radiation intensity at high altitudes, the rate of transpiration under such conditions is often high. It is interesting to note that plants growing in high altitudes are usually dwarfed and often have special structures that tend to reduce water loss.

Soil Factors. Certain soil conditions, such as water content, concentration of the soil solution, composition, and temperature, indirectly influence the rate of transpiration because they affect the rate of water absorption by the plant. If the water content is very low or if the concentration of the soil solution is too high, water cannot be so readily absorbed by the plant. This will ultimately result in decreased transpiration. On the other hand, transpiration rate reaches a maximum value in a soil having only enough water present for good tilth. A greater amount of water in the soil has little if any effect. When the water content of the soil is so low as to cause the plant to wilt, the guard cells of the stomata, along with the other cells of the leaf, lose their turgidity and the stomata close. Once the leaf has started to wilt, therefore, the transpiration rate falls.

Films of dust or of spray materials on leaves in general tend to increase the amount of transpiration. Often the increase is greater at night than in the daytime.

Internal or Plant Factors. As previously stated, the rate of transpiration is also influenced by structural and other features of the plant. It is this fact that makes transpiration different from ordinary evaporation. Because of the great differences in general structure among different species of plants, wide differences in the rate of transpiration between species may occur, even when they are under identical external conditions. Structures that are effective in reducing water loss are usually found best developed in plants growing in dry habitats. Such plants are called **xerophytes**. Many swamp plants also have xerophytic structures because of the fact that the water in a swamp, for various reasons, is not readily available to the plant. Xerophytic structures, while often characteristic of a species, are at least partly a result of the external conditions under which a plant grows. The plant has no ability to develop such structures in anticipation of their need.

Size, Arrangement, and Position of Leaves. The size, arrangement, and position of the leaves of a plant have much to do with the rate of water loss from the plant. Shade plants usually have broad, thin leaves. The rate of transpiration from such leaves is usually high, but this does not cause wilting because of the abundant supply of water ordinarily available in shaded places. The same species of plant growing in direct sunlight often

develops a much reduced leaf surface from which the absolute amount of water lost in a given time is considerably lower. Many shade plants, however, are not able to survive in direct sunlight. Plants that are commonly found in dry situations (xerophytes) practically all have a reduced leaf surface. In many of the cacti the leaves are mere spines. A less modified type of xerophyte leaf occurs in pines and spruces. The leaves of these plants are needle-like in form. A similar reduction in exposed leaf surface is often brought about by the rolling or folding of the leaves. This is frequently seen in the corn plant on hot, windy days or in the folding together of the leaflets of the clover plant under similar conditions. Such positions of leaves tend to reduce transpiration. The same thing results from the edgewise position of leaves toward the sun that is found in the so-called "compass plants."

Leaf Structure. The general structure of the leaf in particular, and of other plant organs as well, influences the rate of transpiration. The epidermis is particularly effective in cutting down transpiration, since, with its cuticle, it presents an almost impassable barrier against water loss. Removal of the epidermis results in rapid wilting. In plants exposed to conditions conducive to excessive transpiration, a double layer of epidermal cells, one or more layers of hypodermal cells, or a thicker cuticle is often developed, particularly on the upper leaf surface. Evergreen plants usually have highly cutinized leaves, and the same is true of arctic and alpine plants. Submersed water plants, on the other hand, develop a very thin epidermis with no cuticle at all. Such plants wilt immediately on being exposed to air. In some cases waxy, resinous, or hairy coverings are found over the epidermis. These also tend to cut down transpiration. In stems, waterproof suberin takes the place of cutin in the outer corky layers of the bark.

The number of air spaces in the leaf and the general compactness of the mesophyll are also important structural features. In general, the looser the structure, the more readily is water lost from the leaf because of the greater transpiring surface. Xerophytic leaves usually have a very compact mesophyll.

Stomata. The importance of stomata in transpiration has already been indicated. The number, distribution, structure, and condition of the stomata all have their effects on the rate of water loss through them.

The fact that the stomatal openings are slit shaped and relatively small and numerous increases the rate of diffusion through them. This has been demonstrated in a purely physical manner by the use of artificial, perforated membranes. When the pores are very minute and sufficiently close together, it has been found that the velocity of flow of a gas through them varies inversely as the radius or diameter and not as the area of the pore.

In other words, the velocity of flow of water vapor through such pores increases as the diameter of the pore decreases. For this reason, it is conceivable that, with the size and distribution of stomata often found in leaves, the rate of water loss, when the stomata are open, might be almost as great as though there were no epidermis at all present. In any case, the actual losses that have been found are much greater than the areas of the epidermis occupied by stomata (1 to 3 per cent) would lead one to expect to find.

The actual number of stomata per unit of leaf area, as has been mentioned on a previous page, varies in different plants. Obviously, the greater this number, the more readily can water vapor escape when the stomata are open. Leaves with stomata on both the upper and the lower surfaces will lose water more rapidly than those in which the stomata are restricted to the lower surface. Frequently, the stomata are placed in furrows or depressions in the leaf surface as in the pines and other plants (Fig. 31). This allows a pocket of saturated air to be retained just outside the pore and thus checks transpiration.

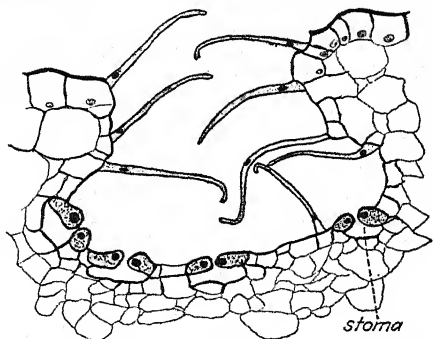


FIG. 31. Stomata sunken in cavity in leaf of *Nerium Oleander*. (Drawing by W. L. Dennis.)

The condition of the stomata, *i.e.*, whether they are open or closed, is obviously very effective. It is chiefly the closing of the stomata in darkness that causes the transpiration rate to be less at night. The closing of the stomata when wilting begins also checks further water loss. It should be emphasized again that the opening and closing of stomata are governed entirely by physical and chemical conditions and that the plant has no control over them. In fact, it frequently happens that at times when the loss of water might prove most harmful to the plant the stomata are wide open.

Water-retaining Ability of Transpiring Tissues. The water-retaining ability of the tissues of the leaf and of other transpiring organs is a very important internal factor which influences water loss. In all living plant tissues there are found hydrophilic colloids, *i.e.*, substances that absorb and hold water by imbibitional force. Some of the water held by these colloids is bound water, which, unlike the free water in the tissues, cannot easily be removed. The degree to which such colloids develop in the plant has much to do with the rate and ease of water loss from the tissues and hence with the ability of the plant to withstand drought. The develop-

ment of hydrophilic colloids is determined partly by inherent characteristics of the plant and partly by external conditions. Some plants fail to develop them under any conditions. Such plants are usually killed by drought, through excessive transpiration. Other plants will develop them if gradually subjected to drier and drier conditions and hence are drought-resistant. The selection of drought-resistant varieties of crop plants is very important in semiarid regions. The best development of hydrophilic colloids is found in many desert plants, such as the cacti. It is this fact that enables such plants to survive under xerophytic conditions that would prove fatal to ordinary plants.

A similar relationship exists between the water-holding ability of plants and their winter hardiness. The effect of freezing is somewhat similar to that of drying, since in both cases water is removed from the living tissues to the detriment of the plant. The presence of sufficient bound water is probably one of the most important factors that enables plants like wheat, planted in late autumn, to survive the winter and enables other species of plants to live in arctic and alpine regions.

Age and Maturity of the Plant. The rate of transpiration varies as the plant matures. In annual crop plants it begins at a slow rate in the seedling, gradually rises to a maximum a little beyond the middle of the growth period, and then gradually decreases until the plants are harvested. Probably one-half of the total water absorbed by a plant during its growing season is transpired during the development of its maximum leaf area. In corn, this occurs during the tasseling and earing period. Corn loses half of the total water lost during the life of the plant in a 5-week period embracing this time of tasseling and earing. It has been estimated that during a 10-day period of maximum transpiration (usually in July) our annual crop plants lose about one-fourth of the total water lost during the whole season. Naturally this is a very critical period in the life of the plant. If the weather is dry during this period of maximum transpiration, it greatly reduces growth and seriously curtails yields.

Disease and Injury. Finally it may be mentioned that disease and injury often increase the rate of transpiration by exposing, to drying out, tissues that normally are protected. For this reason, leaves attacked by fungi or insects frequently wither and die. In some diseases, bacteria or fungi may clog the vascular tissues and thereby interfere with the water supply to the leaves. In other cases, chemicals and toxic substances may be produced by a parasite or structural changes may occur in the parasitized tissues which result in a changed rate of transpiration.

Amount of Transpiration. From the previous paragraphs it is clear that the amount of transpiration varies greatly not only in different kinds of plants but also in the same plant at different times and under different

conditions. It is therefore impossible to state precisely how much water a plant will lose unless we actually determine the loss under controlled conditions. We can, however, get a general idea of the magnitude of the loss by examining the data obtained by different workers with different plants. In the table shown below are given the rates of transpiration of fruit trees and several other species, as determined by the potometer method, using only leafy shoots.

TRANSPIRATION RATES OF TREES AND SHRUBS WITH EDIBLE FRUITS OR NUTS

Common name	Genus and species	Variety	Transpiration rate, cubic centimeters per square inch per hour		
			Day	Night	Average day and night
Apple.....	<i>Pyrus malus</i>	Grimes	0.0341	0.0256	0.0306
Pear.....	<i>Pyrus communis</i>	Kieffer	0.0320	0.0066	0.0217
Peach.....	<i>Prunus persica</i>	Elberta	0.0048	0.0042	0.0045
Cherry.....	<i>Prunus cerasus</i>	Montmorency	0.0183	0.0081	0.0141
Quince.....	<i>Cydonia oblonga</i>	Champion	0.0350	0.0186	0.0242
Gooseberry.....	<i>Ribes grossularia</i>	Poorman	0.0161	0.0094	0.0117
Currant.....	<i>Ribes vulgare</i>	Perfection	0.0452	0.0233	0.0308
Blackberry.....	<i>Rubus nigrobacchus</i>	Taylor	0.0434	0.0253	0.0315
Raspberry.....	<i>Rubus occidentalis</i>	Quillen	0.0325	0.0212	0.0252
Pecan.....	<i>Carya pecan</i>	Warrick	0.0069	0.0064	0.0066
Hazel nut.....	<i>Corylus maxima</i>	Daviana	0.0347	0.0237	0.0275
Black walnut.....	<i>Juglans nigra</i>	Ten Eyck	0.0057	0.0049	0.0052

NOTE. For first four, day = 5:00 A.M. to 7:00 P.M.; night = 7:15 P.M. to 5:00 A.M. For last eight, day = 2:00 P.M. to 7:30 P.M.; night = 7:30 P.M. to 6:00 A.M. For last eight, relative humidity = 45 to 60 per cent during day and 61 to 65 per cent at night and temperature 75°F. during day and 68 to 73°F. at night. Measurements made in July, 1927, weather "clear." Data from *Univ. Ill. Agr. Exp. Sta., Bull. 341*, by Victor W. Kelley.

The figures in this table seem small because the water loss is figured on the basis of a square inch of leaf surface. It is only when the figures are calculated on the basis of the loss per plant or per acre of plants that the great magnitude of the water loss becomes evident. Thus, if we assume that a mature apple tree has 100,000 leaves, that each leaf has an area of 5 sq. in., and that there are 40 trees to an acre, the average rate of 0.0306 cc. per square inch of leaf surface per hour, given in the table for the Grimes variety, amounts to 15,300 cc. or about 4 gal. per tree per hour, 96 gal. per tree per day, 2,880 gal. per tree per month, and 480 tons of water per acre per month. It should be borne in mind, however, that these figures are only approximate, since the rates were determined for

leafy shoots removed from the tree. In any case, the loss is very great. Similar large losses have been reported for other plants. Thus grass plants have been found to lose 6.5 tons of water per acre daily during the summer. A single sunflower or corn plant has been found to transpire 440 lb. of water during the total vegetative period.

Sometimes a comparison is made between the total amount of water transpired and the total dry weight of the plant. The value obtained by dividing the weight of the water transpired by the dry weight produced is called the **water requirement** of the plant. Stated in other words, it is the number of pounds of water used by the plant in producing 1 lb. of dry matter. This value varies greatly in different plants and in the same plant under different conditions but usually has a value of 200 to 500 for most crop plants growing in humid regions. The accompanying table gives some of the values actually found for different plants.

WATER REQUIREMENTS OF PLANTS

In units of water transpired for each unit of dry matter produced

Millet.....	310	Pumpkin.....	834
Corn.....	368	Cotton.....	646
Wheat.....	513	Alfalfa.....	831
Oats.....	557	Red clover.....	453
Potatoes.....	636	Pigweed.....	287
Cucumbers.....	713	Ragweed.....	948

Is Transpiration Useful or Harmful to the Plant? The enormous loss of water resulting from transpiration has led many plant physiologists to doubt whether this process is at all beneficial to the plant. To many it seems wholly injurious. It is probably true that more plants perish from excessive water loss by transpiration than from any other cause and that in many cases it is undoubtedly injurious, even though it may not cause death. Those who ascribe a definite function to transpiration have attempted to point out several ways by which the process might be useful or even necessary to the plant. Most prominent among these have been the relation of transpiration to the absorption and transfer of inorganic substances, its importance in the ascent of sap, and the possible cooling effect it may have.

It has often been stated that the more water a plant loses by transpiration the greater will be the quantity of inorganic substances absorbed by its roots. This idea is based on the false assumption that the inorganic substances are swept in with the water from the soil solution. It has been shown, however, that the inorganic substances enter the root altogether independently of the movement of water and hence could not be greatly affected by the rate of entrance or the rate of loss of water, except in so far as these factors would affect the relative concentrations of the several inorganic substances inside and outside the root. If water were lost to such an extent as to increase the concentration of inorganic substances within the plant, by the laws of diffusion this would decrease rather than increase the rate of absorption and might actually lead to a loss of inorganic substances to the soil solution. Furthermore, if transpiration caused an increase in mineral-salt absorption, we should expect to find higher percentages of inorganic substances in plants subjected to rapid transpiration, but experimental evidence does not support this. In fact, it has been found that some

plants absorb more mineral salts in the shade, when transpiration is low, than they do in direct sunlight, when transpiration is high.

After the inorganic substances are absorbed by roots, it is generally believed that they are transferred to the xylem and carried up from roots to leaves in the so-called "transpiration stream." It is possible that, once the inorganic substances are in the conducting channels, they may be transported by this mass movement, which would be facilitated by transpiration. It is probably true that, if the inorganic substances traveled by diffusion alone, it would take them so long to arrive at the top of the water column in a tall tree that the upper parts of the tree might not receive them at a fast enough rate to supply their needs. On the other hand, if the mineral salts were rapidly removed from the roots by a mass movement in the transpiration stream, a high rate of transpiration should lead to a greater absorption of mineral salts by the roots, because of the relatively greater concentration of these salts in the soil solution under these conditions, but this again has not been found experimentally to be true. Whether transpiration is necessary for the proper movement of inorganic substances through the plant will not be definitely known until the precise method by which these substances are transported in the plant is established.

The most acceptable theory concerning the manner in which sap is raised to the top of the tallest trees assumes that transpiration is the force which creates the pull, at the top of the column, which lifts the sap. There is hardly any doubt that transpiration is an effective cause of the movement of large quantities of water upward in a stem. It is also true, however, that, if there were no transpirational loss, so much water would not need to move up to replace it. The water actually used by the plant in photosynthesis, growth, and other processes would cause a sufficient deficit to create a pull on the water column adequate to supply the plant with its physiological needs. In other words, the sap would probably be lifted whether transpiration took place or not.

Perhaps the most widely accepted possible function of transpiration is that it keeps the plant cool by dissipating the excess energy absorbed when the plant is in direct sunlight. As has been previously mentioned, a large part of the energy incident on a leaf is absorbed. If all of this energy were transformed into heat that could accumulate in the tissues, the plants would rapidly be killed in direct sunlight. The vaporization of water in transpiration involves the transformation of a large part of this absorbed energy and does, therefore, have a cooling effect, just as it does when water is allowed to evaporate from the hands. It does not necessarily follow, however, that transpiration is necessary to keep the temperature of the plant down. The plant tends to acquire the temperature of the atmosphere around it. If the temperature of the air is lower than that of the plant, the plant will radiate heat to the atmosphere. If, therefore, the plant should become heated through absorption of radiant energy, it, like any other heated object, immediately begins to reradiate this energy to the atmosphere around it. For this reason, the temperature of the plant will rise markedly only when, for some reason, such as placing a bell jar over the plant or enclosing the leaves in cellophane or other materials, the reradiation from the plant is interfered with or the air immediately surrounding the plant becomes heated. It is altogether possible that some plant organs are not able to pass off energy as rapidly as they receive it. Such plant parts would be injured in a strong source of radiant energy. Transpiration might be an effective aid in keeping them cool; yet the actual loss of water which occurs under the influence of intense radiation often is a more important cause of injury and death than is the increased temperature. The greatest temperature difference that has been observed between leaves rapidly transpiring in intense radiation and those in which transpiration was checked by coating the leaves with vaseline

is only 2 to 5°C. If transpiration were necessary in order to keep plants cool during intense radiation, we should expect to find an especially high rate of transpiration in desert plants. On the contrary, however, such plants usually have structures that tend to reduce transpiration.

From what has been stated it is obvious that whether transpiration is useful or always harmful to the plant cannot yet be adequately answered. That it is sometimes harmful is certainly true. That it may be of some use to the plant is also likely. So long as the stomata of the leaves are open during the exchange of gases in photosynthesis, the escape of water vapor from the moist, exposed cells of the mesophyll must necessarily occur. The rate at which this occurs and the conditions resulting from it in the plant certainly influence the growth and development of the plant, regardless of what interpretation is placed on the process.

Guttation. Transpiration is the giving off of water in vapor form. Water is sometimes exuded from uninjured plants in liquid form. This process is called guttation. Guttation occurs under atmospheric conditions that normally check transpiration. It is particularly pronounced on cool, humid nights following hot days. The water usually forms in drops along the edges or tips of leaves, where it is frequently mistaken for dew. Usually the water of guttation is exuded through special structures of the leaves known as **hydathodes**. Hydathodes may be simple epidermal outgrowths consisting of one or at most a few cells or they may be rather complex, multicellular structures connecting with the vascular system of the leaf and terminating in a so-called "water pore" resembling a fixed stoma. Guttation also occurs from fungi and other lower plants.

The amount of water given off by plants in this manner varies greatly with different plants and under different conditions. In some species of *Colocasia* more than one hundred drops per minute have been observed. In most plants, however, the rate is much lower. The water exuded contains small amounts of organic and inorganic salts. The physiological significance of guttation is not well known.

LEAVES OF UNUSUAL FORM AND FUNCTION

Some leaves or parts of leaves have peculiarities in form and in function which we do not ordinarily associate with leaves. These unusual types may be so greatly altered in appearance that upon superficial examination they are not recognized as leaves. While the best criterion for the identification of a leaf as such is its morphological origin and development in the bud, highly modified leaves when mature can usually be recognized by their positions at stem nodes, the presence of axillary buds, or the presence of recognizable leaf parts such as stipules. Examples of unusual leaves are numerous. Attention is called to some of the common ones.

Storage Organs. In certain perennial monocotyledonous plants such as the lily and the onion, food manufactured during one growing season is stored up for use during the next growing season in the leaf bases. The

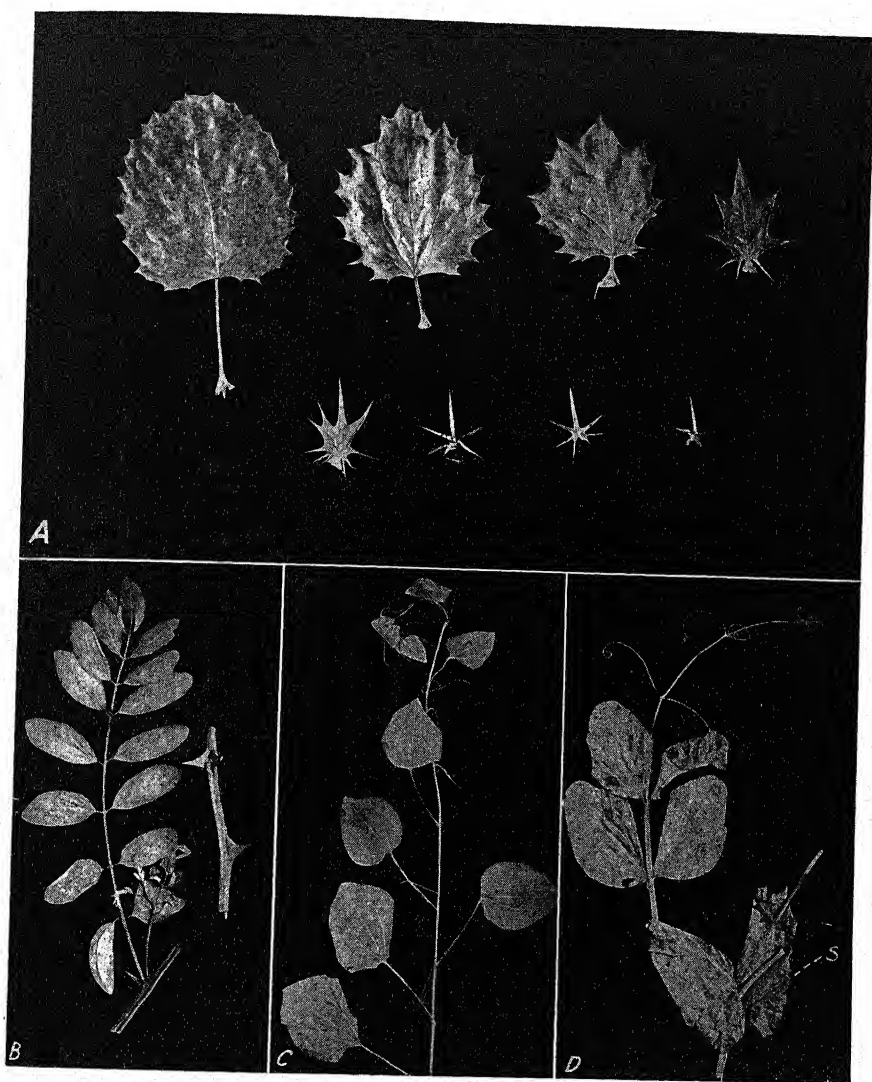


FIG. 32. Leaves of unusual form. *A*, leaves of common barberry (*Berberis vulgaris*), all taken from the same plant, showing gradations from an ordinary leaf with spiny margin to one consisting entirely of spines; *B*, thorns of the black locust, and *C*, tendrils of *Smilax*, both of which are stipules; *D*, leaf of garden pea (*Pisum sativum*) in which the stipules, *s*, are unusually large, assuming much of the photosynthetic activity of the leaf; the tendrils are leaflets.

concentric layers of the onion bulb are the greatly swollen, sheathing leaf bases of the long, green cylindrical leaves, attached to a much shortened stem axis (Fig. 87, *A-B*). The green portion of the leaf carries on photo-

synthesis, and some of the manufactured food is stored in the base of the leaf, which persists as a storage organ after the green portion dies. These fleshy, sheathing leaf bases together with the short stem axis to which they are attached form the onion bulb. When the bulb grows later, the scales lose their stored food and along with it their softness and succulence and are left as thin, dry, dead husks.

The seed leaves, or cotyledons, of many plants such as the garden pea and the bean also serve as food-storage organs. These are described in more detail in the sections on seeds and seedlings.



FIG. 33. Leaf of *Bryophyllum* showing new shoots developed from adventitious buds in the notches in the margin. (Drawing by F. Brown.)

Much thickened green leaves such as those of *Haworthia* and species of *Sedum* have water-storage regions consisting of comparatively large parenchyma cells with big central vacuoles containing hydrophilic colloids.

Bud Scales. Leaves or parts of leaves in the form of bud scales which protect the developing shoot ensheathed by them are present on many of our woody perennials (Figs. 54; and 56, *B*). Bud scales are small, thick, corky structures, often resinous and sometimes hairy. They are usually modified leaf blades, but in some cases petioles, and in others stipules.

Spines or Thorns. In the common barberry some of the leaves are reduced to branched thorns or spines which are recognizable as leaves by their position on the stem and by the presence of axillary buds. Moreover, on almost every leafy branch all gradations may be seen from ordinary leaves with bristly teeth along the margins to thorns (Fig. 32, A), which is further evidence that the thorns are really modified leaves. In some cacti all the leaves are reduced to spines and the photosynthetic function is carried on entirely by the stems. In other plants, as on the black locust (Fig. 32, B), the spines represent only the stipules of the leaf. Not all spines are modified leaves. Those of roses are merely epidermal outgrowths and those of the honey locust are modified stems.

Tendrils. Tendrils are slender, elongated thread-like structures which either twist around various supporting structures or are provided with small disks by means of which they adhere to supports. Many tendrils are transformed stems, but some represent leaves or leaf parts. The terminal leaflets of the garden pea (Fig. 32, D), for instance, develop into tendrils, while the lower ones are typical foliage leaflets. In a certain European vetch all the leaflets are missing and the end of the petiole develops into a tendril. The stipules on this plant become enlarged and look like leaf blades. In some species of *Smilax*, on the contrary, the stipules are tendrils (Fig. 32, C) and the other parts of the leaf are not modified.

Vegetative Reproductive Organs. The leaves of *Bryophyllum* (Fig. 33), if removed from the parent plant and placed on moist soil, are capable of giving rise to buds in the leaf notches. These buds develop into new plants. Certain leaves of the walking fern will take root at their tips and form new plants. These leaves perform the function of vegetative propagation.

Insect Traps. Finally may be mentioned the unusual leaves of insectivorous plants such as the sundew and the pitcher plant (Figs. 35, 36). These are described in the chapter on metabolism and will not be considered further here.

CHAPTER 5

METABOLISM—FOOD SYNTHESIS

In all living organisms there is an unceasing procession of chemical reactions and processes which lead to fundamental internal changes. Living substance is constantly being torn down and built up; the general activities of protoplasm are being maintained; waste products are being eliminated, and a vast amount of energy is constantly being expended. The sum total of these processes and changes is called **metabolism**. Since the ultimate seat of this activity is the cell, we may define metabolism as the sum of the processes concerned in the building up and tearing down of protoplasm. This capacity for metabolic activity is one of the features distinguishing living protoplasm from all nonliving substances.

PLANT FOODS

General. It is obvious that, if an organism is to make new cells or to expend energy in the maintenance of life, it must be supplied with working material. This material is obtained in the form of food. Foods are substances which can be used by the organism either as a source of energy or directly for the building of protoplasm. It is important for the student to realize that the food of the higher plants is exactly the same as the food of animals and consists in every case of organic compounds. The strictly inorganic mineral salts which a plant obtains from the soil and which are added to the soil in the form of fertilizers are often incorrectly called foods. Such substances, while very important to the life of the plant, are used neither as a source of energy nor directly for the building of tissues and therefore are in no sense to be considered as foods. The actual foods of the plant, like those of animals, can be divided into three groups of compounds, *viz.*, **carbohydrates**, **fats**, and **proteins**. As regards foods, chlorophyll-containing plants differ from animals in that they manufacture their own food within their tissues, while animals obtain their food either directly from plants or from other animals which feed on plants. A knowledge of some of the characteristics of the principal plant foods is essential to an understanding of how these substances are made and used by the plant.

The Carbohydrates. Carbohydrates are compounds consisting of carbon, hydrogen, and oxygen, the hydrogen and oxygen being usually in the same proportions as found in water. Most of the carbohydrates commonly found in plants contain 6, or

multiples of 6, carbon atoms and a like number of oxygen atoms less 1 for each group of 6 carbon atoms above the first. Those that contain only 6 carbon atoms are called **hexoses** and have the general formula $C_6H_{12}O_6$. Of less common occurrence in plants, and derived usually by the breaking down of more complex compounds, are the **pentoses**, which are carbohydrates consisting of 5 carbon atoms and having the general formula $C_5H_{10}O_5$. The two most common pentoses found in plants are *arabinose*, obtained from the gum of cherry trees and peach trees, and *xylose*, obtained from other wood gums and from grains, fruits, and straws.

A carbohydrate containing 5 or 6 carbon atoms or less is known as a **monosaccharide**. When the molecule is made up of 2 monosaccharide molecules, the carbohydrate is called a **disaccharide**; when it consists of 3 monosaccharide molecules, a **trisaccharide**; and when it consists of many monosaccharide molecules, a **polysaccharide**. The monosaccharides and disaccharides are readily soluble in water, have a sweet taste, and are known as **sugars**, while the polysaccharides are mostly insoluble in water, are tasteless, and include such compounds as *starch*, *glycogen*, *inulin*, *cellulose*, and *hemicelluloses*. Trisaccharides are less common in plants than other types of carbohydrates. The trisaccharide *raffinose*, $C_{18}H_{32}O_{16}$, occurs in cotton seeds, barley, beet roots, and in other plants.

Of all the monosaccharides found in plants, *glucose*, or *dextrose* and *fructose*, or fruit sugar, are the most common. Glucose, $C_6H_{12}O_6$, is probably found in every living plant cell. It is manufactured directly by the plant and is the most common transport form of carbohydrate. Many of the other carbohydrates and fats are probably changed to glucose before they are transported from one part of the plant to another or before they are broken down in respiration or built into protoplasm. Glucose and fructose are probably the most common substances used in respiration as well as the basic material out of which many of the more complex chemicals in the plant are manufactured. Fructose, $C_6H_{12}O_6$, has the same empirical formula as glucose but differs from the latter structurally and chemically. It is often found with glucose and is particularly abundant in sweet fruits. It is used by the plant in much the same way that glucose is used.

Sucrose, or cane sugar, $C_{12}H_{22}O_{11}$, is the most widely distributed disaccharide found in plants. It occurs particularly in sweet fruits, in stems, seeds, roots, bulbs, and in the sap of many trees like the maple. It is the common table sugar, the commercial product being obtained almost exclusively from sugar cane and from sugar beets. In the plant it is always a storage form of carbohydrate. It is readily soluble in water. On being hydrolyzed (*i.e.*, broken down by the chemical addition of water, as in digestion) it yields one molecule of glucose and one of fructose for every molecule of sucrose.

Other disaccharides of less common occurrence in plants include *maltoose*, obtained chiefly by the digestion of starch but also found as such in leaves, rhizomes, or roots of some plants, *cellobiose*, resulting from the hydrolysis of cellulose, and *trehalose*, which is found widely distributed in fungi. Each of these disaccharides, though structurally different, yields 2 molecules of glucose on hydrolysis. The general formula $C_{12}H_{22}O_{11}$ applies to all of them.

The polysaccharide *starch*, $(C_6H_{10}O_5)_n$, is the commonest storage form of carbohydrate found in plants. It may be found in any part of the plant but is found in greatest abundance in such storage organs as roots, tubers, and seeds. In the grains of cereals it may form from 50 to 70 per cent of the dry weight, and in potato tubers from 15 to 30 per cent of the dry weight. It always occurs in the form of small white grains, the starch grains. In storage tissues of the plant these grains begin as small

leucoplasts, which increase in size as more starch is laid down in them. The full-sized grain displays the original core, called the hilum, surrounded by rings or striations of different densities showing where additional layers of starch were laid down. In the leaf, starch is deposited in the chloroplasts. Starch grains have characteristic shapes and markings which differ with the species of plant in which they are found.

Starch is made by the plant from glucose, which alone it yields on complete hydrolysis. When heated in water, it forms a translucent paste. It gives a characteristic blue color with iodine solution. Since it is insoluble in water, it must always be changed back to sugar before it can be moved out of the cell or used in any way by the plant. Some plants, and particularly many of the monocotyledons, do not make starch but store their carbohydrates in the form of sugar.

Glycogen, $(C_6H_{10}O_5)_n$, sometimes called animal starch, resembles starch in many of its properties. Like starch, it yields only glucose on hydrolysis. Unlike starch, it gives a red to brown color with iodine solution. It is widely distributed in the animal kingdom but has a restricted distribution in plants, being found chiefly in fungi and especially in yeast. It also occurs in some of the algae.

Inulin, $(C_6H_{10}O_5)_n$, differs from starch and glycogen in that it yields only fructose on hydrolysis. It is found in many kinds of plants but is especially abundant in the tubers of dahlia and artichoke and in other composites. It is a common reserve food in these plants.

Cellulose, $(C_6H_{10}O_5)_n$, is another polysaccharide of great importance, often comprising about one-half the dry matter of certain parts of plants. Cotton often consists of over 90 per cent cellulose. It is the principal material used in building the framework of plants and is found in the walls of all plant cells, giving them a rigidity not found in animal cells. Cellulose has the same basic or general formula as starch but is very much more complex. It is probably the most insoluble of all the carbohydrates. It is not only insoluble in the plant but also more or less indigestible and therefore, except in the case of certain bacteria and fungi, is seldom used as a food. It is probably made from glucose, which alone it yields on hydrolysis. Cellulose is frequently found combined with other substances and especially with lignin, with which it forms *lignocellulose*, the common strengthening material of the cells of wood.

The *hemicelluloses* are a group of compounds of varying composition, resembling true cellulose in their physical properties but unlike cellulose in their chemical properties. While insoluble in water, the hemicelluloses are readily soluble in alkali. Like cellulose, they are frequently found in the walls of cells, imparting to these walls strength and toughness. Unlike cellulose, they are at times digested by appropriate enzymes in the plant and hence may be used to some extent as reserve foods. On hydrolysis they yield one or more monosaccharides which may be hexoses or pentoses. Hemicelluloses are found in many seeds, especially those of members of the palm and lily families, in the wood and leaves of many trees, and in some fungi. There are several different kinds of hemicelluloses, the distribution of each of which varies considerably in the plant kingdom. Vegetable ivory, obtained from the seeds of a palm and used in making buttons, umbrella handles, and other articles, owes its properties largely to the hemicelluloses of which it consists.

In addition to the carbohydrates already mentioned, many other substances that are commonly classed with the carbohydrates or yield carbohydrates on hydrolysis are found in plants. Common among these are *gums*, *mucilages*, *pectins*, and *glycosides*. As these compounds are not extensively used as foods by the plant, they need not be considered here.

Fats and Oils. Fats and oils, like carbohydrates, consist of carbon, hydrogen, and oxygen, but these elements never occur in the same relative proportions as found

in the carbohydrates. There is always less oxygen and relatively more carbon and hydrogen in the fats. The chemical properties are in no way similar. Fats that are liquids at ordinary temperatures are known as "oils." In plants the fats commonly exist in the form of oils. Two kinds of oils may be distinguished, *viz.*, *fixed oils* and *volatile oils*. The fixed oils have no particular odor or taste and are the only kinds classed as foods. The volatile oils, as the name implies, are volatile when exposed to air and have very characteristic odors. Common examples of volatile oils are oil of wintergreen, lemon oil, mustard oil, oil of turpentine, and oil of peppermint. The volatile oils have a varied composition which always differs from that of fixed oils. Since the volatile oils are probably never used as foods, we need not consider them further at this time.

The *fixed oils* and *fats* have very characteristic properties. They always leave a permanent grease spot or translucent mark on paper. They are insoluble in water, but easily soluble in ether and in chloroform. They are all lighter than water, their specific gravity ranging from 0.875 to 0.970. When treated with sodium hydroxide, NaOH, or potassium hydroxide, KOH, they saponify; *i.e.*, they form glycerol and soap, which is the sodium or potassium salt of a fatty acid. They are all made up of glycerol, $\text{CH}_2\text{OH}-\text{CHOH}-\text{CH}_2\text{OH}$, and fatty acids. The fatty acids are organic acids having the general formula $\text{C}_x\text{H}_y-\text{COOH}$. Two of the commonest fatty acids found in vegetable oils are palmitic acid, $\text{C}_{16}\text{H}_{32}-\text{COOH}$, and oleic acid, $\text{C}_{17}\text{H}_{33}-\text{COOH}$. The manner in which these fatty acids unite with glycerol to form fats is taken up later under fat synthesis.

Fats and oils are found in greatest quantity in storage regions of plants and particularly in seeds but are also a necessary part of every living cell. They are much more efficient storage foods than carbohydrates, a given amount of fat yielding $2\frac{1}{4}$ times as much energy as the same quantity of carbohydrate. This is because of their relatively higher carbon content and relatively lower oxygen content. For the same reason they require a relatively larger volume of oxygen for their complete oxidation than do carbohydrates. They are readily converted into carbohydrates in the plant and are used chiefly as a source of energy in respiration.

The Proteins. The proteins are among the most complex and most important organic compounds found in plants. Besides being classed as foods, they form an integral part of protoplasm and hence are present in every living cell. The nucleus of the cell is largely protein. Proteins are always found in abundance where there is active cell division and growth. When stored as reserve food in such organs as seeds, they serve chiefly as tissue or protoplasm builders. Besides carbon, hydrogen, and oxygen, they all contain nitrogen and are thus classed as nitrogenous foods. Many of them contain in addition sulfur and phosphorus. The protein molecules are always very large as seen in the following examples: *gliadin* (a protein in wheat), $\text{C}_{685}\text{H}_{1068}-\text{N}_{196}\text{O}_{211}\text{S}_5$; *zein* (from corn), $\text{C}_{736}\text{H}_{1161}\text{N}_{134}\text{O}_{208}\text{S}_3$; *casein* (from milk), $\text{C}_{708}\text{H}_{1130}\text{N}_{180}-\text{O}_{224}\text{S}_4\text{P}_4$.

Many different kinds of proteins with various properties are found in plants but all are composed of chains of simpler compounds, known as *amino acids*. The complete digestion of a protein, therefore, always yields amino acids. The amino acids are organic acids containing one or more basic NH_2 groups, usually in a very definite position in the molecule. A general formula for an amino acid is $\text{R}-\text{CHNH}_2-\text{COOH}$. Examples of those composing the proteins of plants are *glycine*, $\text{H}-\text{CHNH}_2-\text{COOH}$, and *alanine*, $\text{CH}_3-\text{CHNH}_2-\text{COOH}$. More than 25 different amino acids have been isolated. It will be noticed that they all contain the basic NH_2 group and the acid COOH group. Amino acids can react with each other, the NH_2 group of one combining with the COOH group of another, with the loss of water, to form what is called

the **peptide linkage** ($-\text{CONH}-$). The proteins are basically long chains of amino acids combined in this manner, although other substances often enter into their composition.

Proteins can be detected in plants by means of various color reactions, common among which are the *biuret test* and the *xanthoproteic acid reaction*. In the biuret test a solution of copper sulfate is added to an alkaline solution of the material to be tested. When protein is present, this gives a bluish-violet color. In the xanthoproteic acid reaction a little strong nitric acid is added, which gives a yellow color to protein material. This color changes to orange on the addition of ammonia. It is this reaction that causes the fingers to turn yellow in color when they are brought in contact with nitric acid.

The proteins of plants are most often found in colloidal solution in water. Excessive heat or cold and other agents may cause them to coagulate as the albumen of an egg coagulates on boiling, from which a return to the normal is impossible. In storage regions they may exist in small grains, the **aleurone grains**, somewhat comparable with starch grains, though usually much smaller. Aleurone grains are common in seeds. In the cereals, such as wheat, oats, and corn, they are localized in a single layer of cells next to the seed coat. Proteins as such are not able to pass through plant cell membranes and hence must first be converted into amino acids before they can be removed from storage regions to other parts of the plant where they are needed.

The student should remember that the proteins are preeminently the protoplasm- and tissue-building materials of both plants and animals. They may also be used in the synthesis of many other complex substances such as enzymes and secretions.

THE PHASES OF METABOLISM

It has already been stated that metabolism includes all the processes concerned in the building up and tearing down of protoplasm. The building-up processes comprise the synthesis of all the foods as well as protoplasm and are collectively referred to as the **anabolic phase** of metabolism. The tearing-down processes consist chiefly in the conversion of the foods to soluble and usable forms or in the oxidation of these foods for the purpose of releasing and making available to the plant their contained energy. This is the **catabolic phase** of metabolism. Naturally it is impossible to have the one phase without the other. Both are in operation simultaneously so long as the plant is living. That is, the two phases are absolutely interdependent. For convenience of study, the two phases are considered separately. Under the anabolic phase are considered the synthesis of carbohydrates (photosynthesis); the synthesis of fats and oils; the synthesis of proteins; and, finally, the conversion of these foods into protoplasm itself (assimilation). The catabolic phase is discussed in Chap. 12, under the topics of digestion, respiration, and fermentation.

Types of Plants in Relation to Metabolism. According to the method by which they obtain their foods, all plants can be divided into two classes, *viz.*, **autotrophic plants** and **heterotrophic plants**. The former are the self-nourishing or independent plants; *i.e.*, they make within their tissues

all the foods they need, obtaining only inorganic materials and some form of energy from their environment. There are two kinds of autotrophic plants, the **photosynthetic** group and the **chemosynthetic** group. The former obtain materials from the soil, carbon dioxide from the air, and energy from sunlight. They are all plants that contain chlorophyll and hence can carry on photosynthesis. All the higher green plants as well as the lower vascular plants, bryophytes, and algae belong to this group. The chemosynthetic group differs from the former in that the energy they store in foods is obtained from some chemical source instead of light. They need, therefore, to be supplied only with inorganic materials. The carbon they use is obtained from the carbon dioxide of the air as in the former group. The most important members of this group are certain bacteria. None of them contains chlorophyll. Examples are the hydrogen bacteria, some sulfur bacteria, the iron bacteria, and the nitrifying bacteria. The substances which these bacteria oxidize as a source of chemical energy are, respectively, hydrogen, hydrogen sulfide, ferrous iron, and ammonia.

The heterotrophic plants lack the power to synthesize carbohydrates although most of them can make other foods. They are the dependent plants. In general, they must rely on other plants or on dead organic material for their carbohydrates and must be supplied also with mineral salts. To this group belong all the fungi and such higher plants as dodder and Indian pipe (Fig. 34). The heterotrophic plants in general are plants lacking chlorophyll.

Significance of the Synthetic Ability of Plants. It is the almost unlimited power which plants have of making their own foods that gives them so prominent a place in the universe. Of all living organisms, plants alone are able to make carbohydrates. Out of these carbohydrates is ultimately built all the other organic material used by both plants and animals. That is, it is the building source of all organic structure including our own bodies. Likewise, these carbohydrates are our chief source of energy, not only animal, plant, and human energy but also that energy with which we operate our industries which is obtained directly from coal, petroleum, and wood.

Animals can synthesize some proteins but not all the kinds they need. They must depend upon plants for several of the most important amino acids used in protein building. Plants here again are practically unrestricted. Similarly, animals are very greatly limited in the synthesis of vitamins, the majority of which they must obtain ready made either directly or indirectly from plants.

This ability of plants to synthesize foods out of inorganic materials makes them the connecting link between the mineral and the organic worlds.

PHOTOSYNTHESIS

In the preceding section it was stated that the food of plants consists of carbohydrates, fats, and proteins and that these foods are manufactured by the plant within its tissues. The purpose of the present section is to consider food synthesis in plants. Since the carbohydrates are the materials out of which fats and proteins are made, their synthesis is considered first. Because light is used by the plant in this process, the name **photosynthesis** (a synthesis utilizing light) has been given to it.

Location of the Process. Carbohydrates are made by the plant in the chloroplasts. Any part of the plant that contains chlorophyll and is exposed to light can carry on the process. The outstanding organs of photosynthesis, however, are the leaves. All features of leaves seem to be directed toward their efficiency in carrying on this process. The position and the arrangement of leaves on the stem are such as most effectively to enable them to receive light and air. In form and internal structure, leaves are ideal for the process. They are relatively broad and thin, thus enabling them efficiently to intercept large quantities of light. On the upper surface they have a transparent cuticle and a transparent epidermis which prevent water loss but permit light to pass. Beneath the epidermis of leaves of dicotyledonous plants is the compact palisade mesophyll filled with chloroplasts and so placed as to absorb a maximum amount of the available light. Then the spongy mesophyll, loosely constructed with many air chambers which communicate through the stomata with the outside air, permits an orderly exchange of gases in the process. The stomata themselves are so constructed as to be open in the daytime when photosynthesis can be carried on. The veins, ending in the mesophyll, bring in an abundant supply of water for the process and carry off the food as it is made. It would be difficult to imagine a more ideal structure for photosynthesis. Young stems and other green parts, however, also carry on the process, though not so extensively.

The Raw Materials. From the chemical composition of carbohydrates, it is evident that there must be a supply of compounds containing carbon, hydrogen, and oxygen for their synthesis. All these elements are obtained from just two ordinary compounds, *viz.*, water, H_2O , and carbon dioxide, CO_2 . No other compounds obtained from the exterior are used directly in photosynthesis. Ordinarily, terrestrial plants obtain their water from the soil. It is absorbed by the roots and conducted from them through the stem to the leaf. A special tissue, the xylem, is used for this purpose. As described in Chap. 3, the xylem vessels are essentially a system of very fine tubes beginning in the roots and ending in the leaves and containing branches to all parts of the plant, so that every cell is in close proximity to its water supply.

The carbon dioxide enters in gaseous form from the atmosphere, gaining entrance to the leaf by diffusion through the stomata. Soils ordinarily contain more carbon dioxide than is found in the atmosphere. Whereas the average amount of carbon dioxide in the atmosphere is 3 parts in 10,000 parts of air or 0.03 per cent, soils may contain as much as 5 per cent or more of the gas. The high amounts in soils result chiefly from the respiration of roots and of soil organisms. This gas may be displaced to the surface during heavy rains and thereby increase the concentration of carbon dioxide of the atmosphere near the ground level and in the vicinity of growing plants. It is very unlikely that carbon dioxide can be absorbed by roots and carried up internally to other parts of the plant in sufficient quantity to be of material use in photosynthesis. This is proved by the fact that when carbon dioxide gas is withheld from the aboveground parts of plants, so that the sole source is that absorbed by roots, photosynthesis does not take place in measurable quantity, regardless of how much of the gas is available to the roots.

The method by which carbon dioxide enters the leaf is one of simple diffusion. Air consists of a mixture of several gases. It is one of the laws of diffusion that the rate at which a gas travels from one region to another depends upon the difference in concentration of that particular gas in the two regions, regardless of the percentage of other gases present. Hence, the movement of carbon dioxide is independent of that of other gases, or, in other words, it is not necessary for large volumes of air to be drawn into the leaf in order that the necessary amount of carbon dioxide be obtained. The rate of diffusion is always greater from a region of higher concentration toward one of lower concentration. Such being the case, it is obvious that if the interior of the leaf is to obtain a continuous supply of carbon dioxide from the air, the outside concentration must be greater than that inside the leaf. So long as photosynthesis is going on this condition is met because the carbon dioxide within the leaf is constantly being consumed.

After the carbon dioxide has passed through the stomata and into the air spaces of the spongy mesophyll, it goes into solution in the water in the walls of the chlorophyll-containing cells and then diffuses into the cell cavity where it is immediately taken up by the chloroplasts and used in photosynthesis.

Chlorophyll and Photosynthesis. The general properties of chlorophyll have already been taken up in Chap. 2. There remains to be considered the part that this pigment plays in photosynthesis. From the fact that no photosynthesis can take place in the absence of chlorophyll it is obvious that its role is an important one. Chlorophyll probably takes part in the process in several ways. One of the most important of these is through its absorption of light. White light, as it comes from the sun, consists of a

series of rays of different wave lengths. When a beam of this light is passed through a prism, each of the different rays suffers a different amount of refraction or bending, the longer (red) rays being least refracted and the shorter (blue-violet) rays most. The result is that a spectrum is formed, part of which is visible to the eye and appears as a band of colors consisting of red, orange, yellow, green, blue, and violet, in that sequence. At the red end of this spectrum, but beyond the visible red rays, there is a series of longer invisible rays called the infrared. Similarly, beyond the violet there is a series of shorter, invisible rays called the ultraviolet. If now we place a tube of chlorophyll in the path of the beam of light before it reaches the prism, certain parts of the spectrum are absorbed by the chlorophyll and a continuous band of colors is no longer obtained, but the absorbed portions appear as dark bands. These dark bands are called the **absorption bands** of chlorophyll. The darkest of them will be in the visible red. Others appear in the yellow and in the blue-violet and ultraviolet. Green is least absorbed and hence chlorophyll has a green color. It is significant to note that this part of the spectrum which is absorbed by the chlorophyll is probably the principal light used in photosynthesis. In other words, chlorophyll enables the plant to absorb light for photosynthesis. Since no decrease has been observed in the amount of chlorophyll in leaves during intense photosynthesis, it is likely that chlorophyll may function as a photocatalyst, *i.e.*, a substance which accelerates a reaction in light, appearing unchanged at the end of the reaction. In this connection the chlorophyll may function in hydrogen transfer.

Relation of Light to the Process. Photosynthesis is strictly an endothermic process, *i.e.*, an energy-storing process. The energy stored is the radiant energy of sunlight which is transformed into a potential form in the resulting carbohydrates. Not nearly all of the radiant energy that falls on plants is utilized in the process. To begin with, only the part that is absorbed can be used. In the previous paragraph, it was stated that only certain parts of the spectrum are absorbed. These parts contain only a relatively small part of the total energy contained in the incident light. According to the physicist Langley, who has made a very careful study of the energy of sunlight, the distribution of the energy in the spectrum is as follows:

<i>Spectral region</i>	<i>Percentage of total energy</i>
Infrared.....	62 to 63
Visible.....	37.0
Ultraviolet.....	0.6

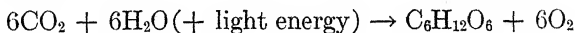
Since none of the infrared is used in photosynthesis, it is clear that 62 to 63 per cent of the total energy has no value in the process. Maximum

absorption occurs in the red part of the spectrum, and the next largest amount in the blue-violet region. Green is not absorbed to any great extent. The total amount utilized varies with different plants. The thicker the leaf, the more light it can absorb, but in general only about 1 per cent of the total energy incident on the leaf is used in photosynthesis. This seems like an insignificant amount; yet it is sufficient to supply practically all of the energy used by man, animals, and plants. The student should keep in mind that it is this storing of energy from an outside source, thereby making it available for use by all forms of life, that makes photosynthesis stand out as the leading synthetic process in nature. All the activities of animals result in the dissipation or loss of energy. Green plants alone, through photosynthesis, are able to add to and build up the biological supply of energy. The storing of energy in photosynthesis is therefore the most significant part of the entire process.

Chemistry of the Process. The problem of how the plant is able to put together carbon dioxide, water, and sunlight to make carbohydrates has attracted the attention of some of the world's best chemists during many years. Probably no other plant process has been more thoroughly studied, yet in spite of all the investigation the exact nature of the process is still unknown. The well-known facts about the process can be stated as follows:

1. Water and carbon dioxide are the raw materials used.
2. Chlorophyll is necessary.
3. Light energy is stored.
4. Oxygen is liberated.
5. Carbohydrates are formed.

Most of these facts are suggested in what is sometimes called the photosynthetic equation:



This is a purely arbitrary equation which probably does not truly represent the actual reactions of the process but merely indicates the raw materials and the end products. It is correct in one detail, *viz.*, it indicates that, for every volume of carbon dioxide consumed, an equal volume of oxygen is liberated, a fact that can be verified by experiment. What the actual steps in the process are has not yet been determined. Many different theories have been advanced. In 1870, von Baeyer, a German chemist, suggested that probably formaldehyde, CH_2O , is formed during the process as an intermediate product and that it is converted into glucose. The formula for formaldehyde indicates that it might be considered as the simplest possible type of carbohydrate. A union of 6 molecules of formaldehyde would give 1 molecule of glucose. This idea had a wide influence on

later investigators with the result that many of the theories advanced consider the formation of formaldehyde as a part of the process. More recent work, however, indicates that it is unlikely that formaldehyde is formed.

A detailed discussion of the possible mechanism of photosynthesis is beyond the scope of a general textbook of botany. It might be said, however, that evidence is accumulating to indicate that the process is fundamentally an oxidation-reduction reaction between carbon dioxide and water involving a number of steps including both chemical and photochemical reactions by which, in the presence of light and of chlorophyll, the carbon dioxide is reduced with hydrogen obtained from water, the oxygen liberated in the process being dehydrogenated water. That the oxygen comes from the water and not from the carbon dioxide, as formerly believed, has been demonstrated by the use of water or carbon dioxide containing heavy oxygen, *i.e.*, oxygen having an atomic weight of 18 instead of the usual 16. By thus "tagging" the oxygen it could be traced through to the end products of the process. Thus, when water containing heavy oxygen was supplied to plants carrying on photosynthesis, the oxygen liberated was found to be heavy oxygen. When carbon dioxide containing heavy oxygen was supplied, the oxygen liberated was the ordinary kind (atomic weight 16), proving that the liberated oxygen was derived from the water.

Products of the Process. In most plants the soluble sugar, glucose, is probably the first stable product of photosynthesis. In many plants this glucose is immediately transformed to starch in the leaf. The advantage of this change is that starch is insoluble in water and therefore does not affect the osmotic properties of the cell. Starch is also less bulky and therefore does not retard the process so quickly through the accumulation of end products. At night the starch is converted back to sugar and is removed from the leaf through the veins to other parts of the plant. The cells of the leaf are thus free of starch in the morning and can immediately begin photosynthesis again. Some plants, particularly many of the monocotyledons like onions and lilies, do not make starch. In that case the carbohydrate may remain in the form of glucose or be converted into sucrose and other carbohydrates. Sucrose, or cane sugar, is formed in the leaves of many plants.

Oxygen is always liberated as a by-product in photosynthesis. The net result of gaseous exchange in the leaf in daytime, therefore, is that carbon dioxide is taken in and oxygen given off. The liberation of oxygen by plants in photosynthesis is the chief method by which the supply of oxygen in the atmosphere is kept constant. Here again plants make life possible for animals and man, since all animals constantly use up oxygen and must have a new supply.

Rate of Photosynthesis and Factors Affecting It. The rate at which carbohydrates are made by the plant depends upon the combined action of external and internal factors. The most important external factors are **temperature, carbon dioxide supply, the kind and amount of light, and the water supply.** Two internal factors are of importance, *viz.*, **the chlorophyll content and a protoplasmic factor.**

Temperature. In general, as the temperature rises above the minimum, the rate of photosynthesis rises in a geometrical way. That is, for every 10° rise in temperature the rate of photosynthesis increases 2.2 to 2.6 times, until a temperature of 30 to 35°C. has been reached, beyond which no further increase in the rate occurs. If the temperature rises very far above 30 to 35°C. , the rate may decrease. As will be seen later, temperature effects are closely tied up with the internal factors limiting the process.

Carbon Dioxide Supply. Probably no other single external factor under natural conditions has a greater influence on the rate of photosynthesis than the carbon dioxide supply of the atmosphere. As previously stated, there is an average of only three-hundredths of 1 per cent of this gas in the air. Careful experiments have shown that plants could use much higher percentages if they were available. When greater amounts are supplied artificially to plants, the rate of photosynthesis increases until a maximum point is reached, beyond which no increase occurs. For many of the common plants this point is reached at a concentration of about 0.5 to 1 per cent of the gas. Some plants probably could utilize still higher percentages of carbon dioxide. When it is borne in mind that this carbon dioxide is the only source of carbon for the plant and that carbon makes up about 50 per cent of the dry weight of plants, the importance of an ample supply of the gas becomes apparent. Much has been done to increase yields of farm crops by adding mineral fertilizers to the soil; yet all the minerals in plants combined make up only from 1 to 10 per cent of the dry weight of plants. The application of additional amounts of carbon dioxide to crop plants has been tried by many different investigators and the results have generally been very promising. Increased yields of from 30 to 300 per cent have been reported with such crops as potatoes, tomatoes, beets, carrots, and barley. The small percentage of carbon dioxide in air makes it likely that it is this factor that ultimately determines how fast photosynthesis can go on in the plant under natural conditions, although it is likely that the concentration of carbon dioxide of the air near the ground level is always higher because of its escape from the soil.

The Kind and Amount of Light. Light is one of the most variable factors in nature. It may vary in quality, in intensity, and in duration, and each of these will affect the rate of photosynthesis. While some photosynthesis can go on under all parts of the visible spectrum and to some extent in the

ultraviolet, not all parts of the spectrum are of equal value. If the spectrum of sunlight is divided at the middle point of the visible region and the product of photosynthesis in the red half is represented by 100, then the value of the blue half would be about 54 or roughly half that of the red. The lowest rate occurs in the green region. Infrared radiation is not used in photosynthesis and the intensity of the ultraviolet portion of sunlight is so low as to make this region also more or less insignificant in the process. While the rate is highest in the red end, owing to its greater energy value in sunlight and to the stronger absorption of light by chlorophyll in this region, absence of the blue-violet end of the spectrum causes a marked lowering of the rate of photosynthesis. It is partly for this reason that photosynthesis proceeds at a lower rate under artificial light, most artificial lights, such as tungsten incandescent lamps, being deficient in blue-violet rays.

As to the intensity of light, if we begin with darkness or a very low light intensity and gradually increase it, the rate of photosynthesis increases as the intensity increases, up to a maximum point. Plants vary considerably as to the location of the maximum point, but for most plants it is far below the intensity of daylight at noon. It has been found that noon daylight intensity during the summer can be reduced to one-twelfth of its value before any decrease in the rate of photosynthesis occurs in individual leaves. This means that there is ordinarily much more light available in nature than plants can use, so long as the other factors such as carbon dioxide supply remain the same.

The duration of the light or the length of time the plant is in the light will obviously affect the amount of carbohydrate that can be made. This factor becomes important during the short days of autumn and winter. It is of considerable practical importance in the production of greenhouse crops in winter.

Water Supply. Water being one of the raw materials out of which the carbohydrates are made, it is easily seen that a deficiency of water might check the rate of photosynthesis. Only when water becomes so low as to cause wilting, however, does this factor become important. Under ordinary growing conditions of plants the water supply seldom becomes a limiting factor in the process.

The Internal Factors. Of the internal factors that affect the rate of photosynthesis only two need be considered here, *viz.*, the chlorophyll content of the leaf and a protoplasmic factor. The protoplasmic factor involves a number of features definitely tied up with the activities of protoplasm and not well understood. The importance of a protoplasmic factor is indicated by the fact that attempts to cause photosynthesis *in vitro* or with chlorophyll extracts have generally proved unsuccessful. Part of the protoplasmic factor probably involves the action of several

enzymes associated with the process. The two internal factors mentioned are best considered together. Both of these factors are closely tied up with temperature relations. The action of enzymes is always accelerated as temperature rises. It may thus be that the increased rate of photosynthesis which results from increased temperature may be due partly, at least, to the speeding up of the action of enzymes associated with the process. Acceleration of the enzymes can lead to increased photosynthesis, however, only when there is an abundant supply of chlorophyll present. In general, the greater the amount of chlorophyll present the higher will be the rate of photosynthesis because more light can then be absorbed. When the chlorophyll content is low, an increase in temperature has little effect on the rate of photosynthesis, because, even though this increase accelerates the enzyme activity, the process cannot go on more rapidly because the chlorophyll is probably already working at maximum capacity and cannot, therefore, absorb the additional light which would be needed to make use of the increased enzyme action. On the other hand, when the chlorophyll content is high, an increase in temperature will have a marked effect on the rate of photosynthesis because there will then probably be a sufficient absorption of light to make use of the increased activity of the enzymes. It is thus possible that in plants high in chlorophyll content the activity of the enzymes may become the factor that limits the rate of photosynthesis, while in plants low in chlorophyll it is the absorption of light that limits the rate.

Limiting Factors. It should be kept in mind that all these factors are operating simultaneously and that the amount of carbohydrate made will depend upon their joint action. Yet, as a chain is no stronger than its weakest link, so the rate of photosynthesis in the last analysis is probably determined by that factor which occurs in minimum. For example, if there is a very favorable temperature, a sufficiently intense light of the proper quality, an abundance of water and chlorophyll, but a very low supply of carbon dioxide, then the rate of the process will be determined by the carbon dioxide supply or, in other words, the carbon dioxide supply operates as the **limiting factor**. Any one of the external or internal factors that have just been discussed may become a limiting factor in photosynthesis.

Quantity of Carbohydrates Made in Photosynthesis. In view of what has been said concerning the effect of different factors on the rate of photosynthesis, it is obvious that the amount of carbohydrate made will vary greatly in different plants as well as in the same plant under different conditions. It is, therefore, impossible to state precisely how much carbohydrate a plant can make in a given time unless we measure it. Such measurements have often been made and average figures have been obtained for general average conditions. Ganong gives as an average for

many common plants 1 g. of carbohydrate per square meter of leaf surface per hour. Some plants will make much more than this and some less. A gram an hour produced by a square meter of leaf surface seems like an insignificant amount; yet when all the plants that carry on the process are considered, this soon adds up to tremendous figures. To illustrate: for the crop season 1930-1931 the world produced 31,977,000 tons of sugar of which the United States alone produced 1,391,693 tons. These figures merely represent the output of two cultivated species of plants, sugar cane and the sugar beet, and in reality are the surplus produced by these plants over and above what they used themselves. In the following table are given the annual yields of several other crops that consist largely of carbohydrates made by photosynthesis.

ANNUAL YIELDS OF CROPS RICH IN CARBOHYDRATES
Ten-year average (1921-1930)

Crop	United States, bushels	World, bushels
Corn.....	2,712,430,000	4,144,000,000
Wheat.....	831,578,000	4,081,000,000
Oats.....	1,285,513,000	4,491,000,000
Barley.....	237,395,000	1,636,000,000
Rye.....	56,269,000	1,664,000,000
Potatoes.....	386,097,000	

The total value of these and other crops averages between 5 and 10 billion dollars per year in the United States alone. When it is remembered that crop plants make up only a small part of the total vegetation of the earth, the vast magnitude of the product of photosynthesis in the aggregate becomes apparent.

Fate of the Products of Photosynthesis. The carbohydrates made in photosynthesis are used by the plant in various ways. If starch is made in the leaf, it is first changed to the soluble carbohydrate glucose and then carried to other parts of the plant through the phloem of the stem. There it may be oxidized at once for its contained energy or it may be transformed into other carbohydrates and related compounds or to fats and proteins. Some of it is used in building new protoplasm and new tissues. After all these needs have been satisfied, there is always a surplus which the plant stores as reserves in such organs as roots, stems, and seeds. It is these stored reserves that are made use of by man in many of his crop plants. These uses may be summarized as follows:

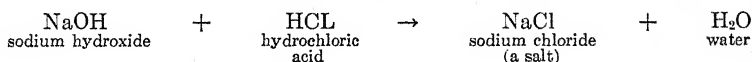
1. Changed to soluble forms (digestion).
2. Carried to other parts of the plant (translocation).
3. Oxidized to liberate energy (respiration or fermentation).

4. Used in the synthesis of fats, proteins, and other compounds.
5. Used in the building of new tissues (assimilation and growth).
6. Carried to storage organs as reserves (storage).

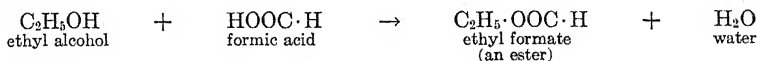
Summary. Photosynthesis is a synthetic plant process by which chlorophyll-containing cells store the radiant energy of sunlight and liberate oxygen in making carbohydrates out of water obtained from the soil and carbon dioxide gas obtained from the atmosphere. Fundamentally the process is one of oxidation-reduction in which carbon dioxide is reduced with hydrogen obtained from water, the oxygen liberated in the process being dehydrogenated water. The rate at which the process goes on is dependent upon such external factors as temperature, light, carbon dioxide supply, and water supply and the internal factors, chlorophyll content, and a protoplasmic factor, any one of which may operate as a limiting factor. The average plant makes about 1 g. of carbohydrate per square meter of leaf surface per hour. This is sufficient to supply all forms of plant and animal life with food. The carbohydrates so made are used by the plant in digestion, translocation, respiration, synthesis of other substances, assimilation, and storage.

THE SYNTHESIS OF FATS AND PROTEINS

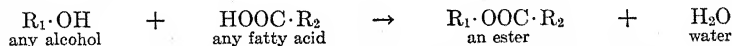
Fat and Oil Synthesis. The general properties of the fats have already been considered. It will be recalled that the fixed oils or fats, which alone are used as food, consist of glycerol and fatty acids; *i.e.*, they are glycerol esters of fatty acids. An ester is an organic salt derived from an organic acid in much the same way that a mineral salt is derived from an inorganic acid and a metallic base. The formation of an inorganic salt is illustrated in the following equation:



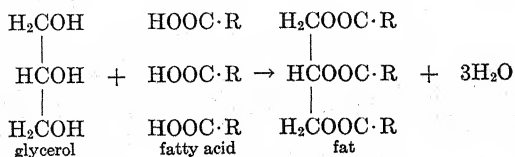
In the same way, the following equation illustrates the formation of an organic salt or ester:



In general,



Glycerol is an alcohol with three OH groups and therefore 3 molecules of a monobasic acid are required to react with all the OH groups. When this happens, a fat or oil is formed as follows:



Many of the oils found in plants contain stearic, palmitic, or oleic acid. It is possible, and in fact usually happens, that two or three different fatty acids may react with a single glycerol molecule in the above reaction.

It is evident from the last equation given that if a plant is to manufacture a fat it must first have glycerol and fatty acids. Hence, both of these substances must be made first. There is reason to believe that they are both made out of carbohydrates through a series of intermediate steps which are not well known. Glycerol is probably made from glucose. The fatty acids are probably made by the fermentation of sugars. Neither light nor chlorophyll is necessary. The condensation of the glycerol and fatty acids to form the fat is brought about by an enzyme called *lipase*. This phase of the process occurs particularly in those parts of the plant where the water content is diminishing, as in developing seeds. It is part of the ripening process in seeds. If the water content remains fairly high, fatty acids and glycerol may remain together as such for a long time without forming fat. The steps in fat synthesis in plants may be summarized as follows:

1. Formation of glycerol by the splitting of glucose or other hexose sugars.
2. Formation of fatty acids, probably by the fermentation of sugars.
3. Condensation of glycerol and fatty acids to form fat, brought about by the enzyme *lipase*.

From the facts that fats are a part of all living protoplasm and that fats as such cannot move from cell to cell, it is likely that all protoplasm is able to synthesize fats or, at least, to carry out the last step in the process.

Fats are used chiefly as a source of energy, their energy value, as explained before, being $2\frac{1}{4}$ times that of carbohydrates. Besides making up a part of all protoplasm, they are commonly found stored in seeds such as flax, peanuts, castor bean, and sunflowers and in the embryo of corn and other cereals. Commercial oils are obtained from each of these types of seed.

Protein Synthesis. The protein molecule always contains nitrogen and usually sulfur, in addition to carbon, hydrogen, and oxygen. Phosphorus may also be present. It is in the making of the proteins that the plant uses many of the minerals which it absorbs from the soil, particularly nitrates, sulfates, and phosphates.

The method by which proteins are made probably varies in different plants. Carbohydrates from the photosynthetic process serve as a source of the carbon, hydrogen, and oxygen. The higher plants generally use nitrates obtained from the soil as their source of nitrogen for the process. Some, however, are able to use ammonium salts. A wide variation exists in the lower plants as to what form of nitrogen they can use. Some of the bacteria can use atmospheric nitrogen; some use ammonium salts; some nitrites and some nitrates. Still others use organic salts of nitrogen. The steps in the process of protein synthesis will therefore depend upon what form of nitrogen is utilized. In higher plants there are probably at least three steps, *viz.*,

1. The reduction of nitrates.
2. The synthesis of amino acids.
3. The linking together of the amino acids to form protein.

How each of these steps is brought about is as yet not well known. The reduction of the nitrates to nitrites and to ammonia is necessary before the second step can take place. This reduction probably occurs in different places in the plant. There is evidence that in apple trees it occurs in the roots, while in plants such as the tomato it has been found to occur in stem tips, in leaf cells, in the cortex of leaf petioles and stems, and near the food-conducting tissues of the stem. The reduction is probably accomplished by enzymes. The energy required for the process is probably obtained

by the oxidation of glucose or fructose. Oxygen seems to be necessary. While light is not necessary for this stage of protein synthesis, it may in some cases affect the rate of the reduction.

The amino acids are next synthesized out of glucose or other sugars and the product of the reduction of the nitrates. This step of the process also probably takes place in different organs of the plant, particularly in leaves and stem tips. Very little is definitely known about the exact manner in which it is brought about. A good supply of carbohydrates is essential. Amino acids can be moved as such from one part of the plant to another and therefore their presence in a given region does not necessarily mean that they were synthesized there. Furthermore, they may be formed in digestion by the splitting of proteins already existing in the plant. This fact makes it difficult to determine where and how amino acids are made in plants. The third step in the process, the linking together of the amino acids to form proteins, is strictly an enzymatic process. This phase of protein synthesis can be carried on by animals as well as by plants. In the plant it may be looked upon as a function of every living cell; yet there are regions in the plant where proteins are made in much greater quantities than elsewhere. Such regions are found in all actively growing points and in developing seeds. The protein content of the wheat kernel, for instance, as it develops on the plant, gradually increases until the grain is dry and mature. In the early milky stage, amino acids are found in abundance. As the water content is reduced through the storage of foods, the amino acids are converted into proteins. In the mature grain, therefore, the percentage of proteins is relatively high, while that of amino acids is very low or nil. In the linking of the amino acids, the NH_2 group of one of them unites with the COOH group of another and thus a whole chain of amino acids results. The proteins are basically such chains of amino acids.

The essential features of protein synthesis in plants are that they are built up of amino acids, which in turn are made out of the carbohydrates produced in photosynthesis and such salts obtained from the soil as nitrates, sulfates, and phosphates. Proteins are an essential part of every living cell, being the chief material out of which protoplasm itself is made.

SUMMARY OF THE ANABOLIC PHASE OF METABOLISM IN GREEN PLANTS

An attempt has been made in the present chapter to show how the plant builds up the various substances that are needed for its existence. Beginning with the inorganic materials, water and carbon dioxide, it first manufactures carbohydrates, a process in which the energy of light is stored for future use. This process, called photosynthesis, is carried on solely by chlorophyll-bearing plants. Out of the carbohydrates thus made are formed most of the other compounds found in plants. Starch, cellulose, and other carbohydrates are made directly out of the original glucose resulting from photosynthesis. Some of the glucose is converted into glycerol and fatty acids from which fats are made. By the addition to glucose of such minerals as nitrates, phosphates, and sulfates, amino acids are made. These in turn are linked together to form proteins. Out of the proteins may be made enzymes, secretions, other complex organic compounds, and protoplasm itself. The making of the living substance protoplasm is called **assimilation**. Assimilation is the ultimate goal of all the

anabolic processes. It is really in assimilation that the nonliving substances become living. It has been stated that the exact mechanism of photosynthesis is not known and that still less is known about fat synthesis and protein synthesis. Almost nothing is known as to how the nonliving substances become living in assimilation except that it can take place only where life already exists. Before any substance can be assimilated, it must be in a soluble form and must be carried to those regions where assimilation is in progress, such as the growing parts of the plant. Since much of the food that is used is stored in an insoluble form, this necessitates that certain breaking-down processes precede assimilation. Such processes constitute the catabolic phase of metabolism. Anabolism and catabolism thus go on hand in hand, simultaneously.

FOOD HABITS OF PLANTS LACKING CHLOROPHYLL

The foregoing discussion has been concerned chiefly with plants that contain chlorophyll, such plants alone being able to carry on photosynthesis. Many plants, however, do not contain this pigment. Prominent among these are the bacteria, the fungi, and such flowering plants as dodder and Indian pipe. It is obvious that such plants cannot carry on photosynthesis. Hence, they must obtain their carbohydrates in some other manner. Since chlorophyll is not needed in the synthesis of fats and proteins, these foods can be made by plants lacking the pigment and are made in the same manner as described previously. As stated in the previous section, we may subdivide plants that lack chlorophyll into two groups, *viz.*, the autotrophic plants, consisting of certain bacteria that use energy obtained from some chemical source instead of sunlight to form carbohydrates, and the heterotrophic plants, which cannot make carbohydrates at all but must obtain them from other organisms, living or dead. A heterotrophic plant that obtains its food from another living organism is called a **parasite**, the organism from which the food is taken being called the **host**. If the food is obtained from a dead or decaying organism, the heterotrophic plant is called a **saprophyte**. The association of the two organisms in the first instance is called **parasitism**, and in the second instance **saprophytism**. A mushroom or a toadstool growing on the ground or on an old log is a saprophyte. Such a fungus as the one causing the late blight of potatoes is a parasite.

The Nutrition of Saprophytes. In the case of saprophytes, the question of obtaining food is relatively a simple one. Such plants are largely confined to the groups of the fungi and the bacteria. These grow directly on the nonliving substance and absorb their food in solution from it. The fungi usually develop an extensive system of vegetative filaments collectively termed the **mycelium**, which grows through the substratum and absorbs the food from it. The bacteria, on the other hand, are one-celled plants, and each cell must absorb its material directly through its own cell membrane.

There are a few cases of flowering plants, such as the Indian pipe (Fig. 34, A), that entirely lack chlorophyll and thus must obtain their carbohydrates from the substratum, although in some such instances these plants are known to be partially parasitic on the living roots of other plants.

The Nutrition of Parasites. Among the parasitic fungi there occurs the same formation of a more or less extensive mycelium noted above for the saprophytic species. Any part of the mycelium may function in absorption of foods. More often, however,

these species have special structures which penetrate the host cells and absorb food directly from these cells. Penetration, particularly in the case of leaf parasites, is often directly through the outer protective cells such as the epidermis. This is secured by the activity of special enzymes secreted by the tips of the mycelium and capable of dissolving out the substances of the cell walls so as to provide a place of entry for the mycelium. Once within the tissues of the host, these parasites often develop special organs for absorbing the food from the living cells, for many parasites enter the living cells and continue absorbing the foods without killing the cells. For this purpose the tips of the mycelium are specialized and become more or less rounded or pouch-like sacs known as **haustoria**.



FIG. 34. Dependent seed plants. *A*, Indian pipe (*Monotropa uniflora*), a saprophytic flowering plant; *B*, common dodder (*Cuscuta* sp.), a twining seed plant parasitizing water willow (*Justicia americana*).

In such parasitic flowering plants as the dodder (Fig. 34, *B*) and the mistletoe, multicellular, greatly modified roots penetrate the host tissues and do the work of absorption. The conducting cells of these parasites unite directly with those of the host so that the relationship is extremely intimate.

It is a well-known fact that parasites are often highly injurious to their hosts. (1) They may extract so much of the food as to leave the host in a starving condition without enough foods to carry on its growth. As a result the host may become considerably dwarfed or may even die. (2) The presence of the parasite may stimulate to extraordinary growth local regions of the host, thus giving rise to various kinds of deformities, such as swellings, galls, tumors, and witches'-brooms. (3) They may throw off highly injurious waste products often known as toxins, which may poison the host and cause its death entirely or at least cause the death of some of its organs. (4) They may penetrate and disorganize the cells or their content directly, resulting

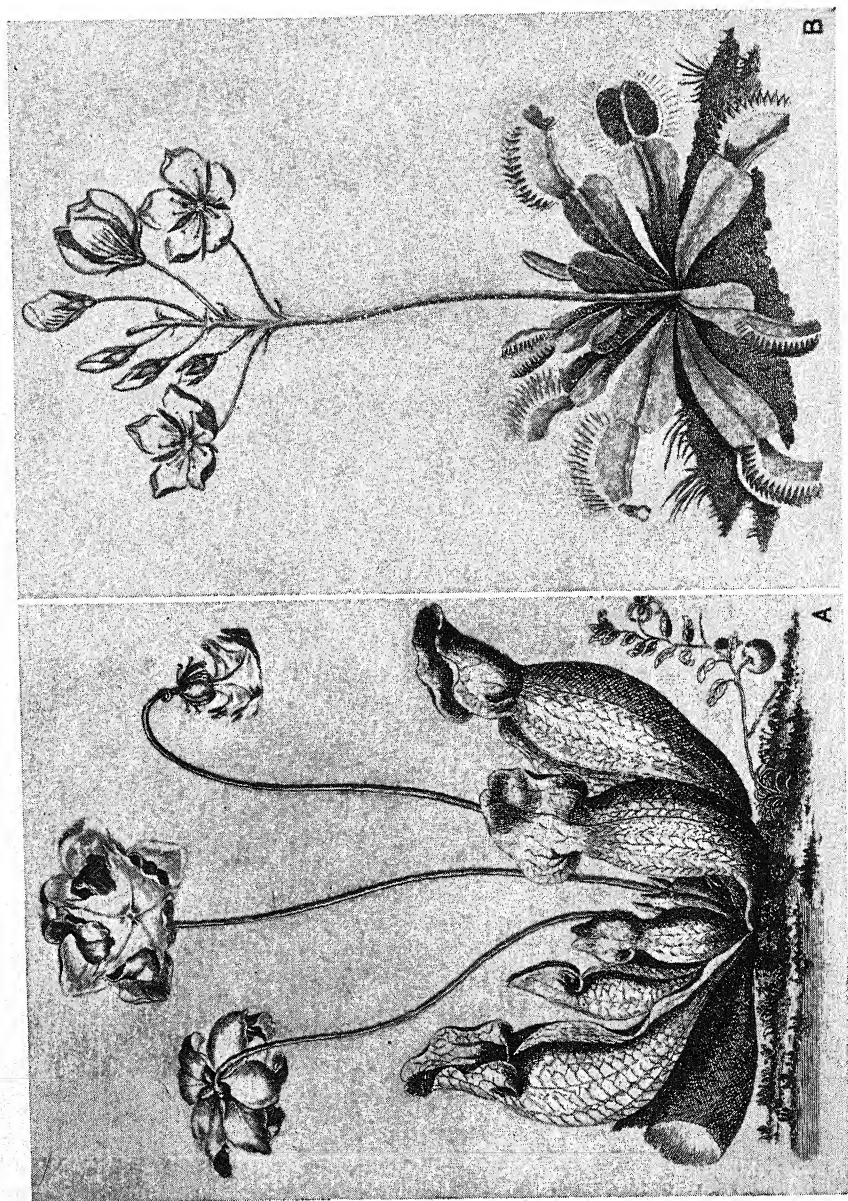


FIG. 35. See legend at bottom of page 97.

in more or less extended death of tissues. In general, the effects of plant parasites on their plant hosts are quite comparable with the effects of plant or animal parasites on animal hosts. It follows that plants may become diseased even as the lower animals and man do. On this basis, a specialized branch of botany known as plant pathology has been developed. Every state experiment station in the United States now has

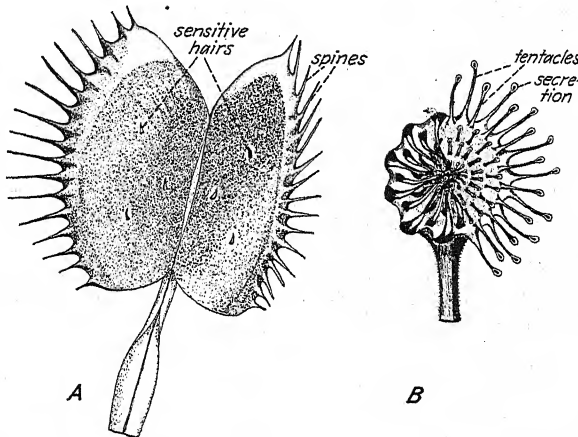


FIG. 36. A, leaf of Venus's-flytrap (*Dionaea muscipula*), enlarged, showing sensitive hairs and marginal spines; B, leaf of sundew (*Drosera rotundifolia*) enlarged, showing tentacles with a liquid secretion at their tips. The tentacles on the left side of the blade have closed over a small insect. (Drawings by F. Brown.)

associated with it one or more specialists in this line of work, whose duties are to investigate these diseases or to disseminate information as to how they can best be brought under control and their ravages prevented.

INSECTIVOROUS PLANTS

In conclusion, a few words may be said concerning a group of plants highly specialized in the manner in which they obtain a part of their food. These have been called **insectivorous plants** because they are able, by one means or another, to trap and devour insects. The insects are usually caught in a special structure which is usually a modified leaf or part of a leaf. By means of enzymes secreted by the specialized leaf structure, the bodies of the insects are digested and the digested products absorbed by the plant.

FIG. 35. A, pitcher plant (*Sarracenia purpurea*), an insectivorous plant found growing in bogs. The leaves consist of hollow receptacles or "pitchers," which are usually partly filled with water in which insects are trapped and drown. B, Venus's flytrap (*Dionaea muscipula*), an insectivorous plant commonly found in southern bogs.

(These two illustrations were taken from the book, "Elements of Botany," by Benjamin Smith Barton, who was one of the early botanists of the United States, a physician, and professor of materia medica, natural history, and botany in the University of Pennsylvania. This book, first published in 1803, was one of the first, if not the very first, textbook of general botany published in the United States. The illustrations in it were almost all taken from drawings by William Bartram, son of John Bartram who was one of the most prominent botanists of America during Revolutionary times.)

The so-called "pitcher plants" (Fig. 35, A) commonly found in bogs belong to this group. These plants are provided with cup-like or pitcher-like devices containing water, into which insects wander and are prevented, by inwardly directed spines and other devices, from getting out again. The insects drown and gradually disintegrate and the digested constituents of their bodies are absorbed by the plant tissues.

The common sundew (*Drosera*) (Fig. 36, B) and the Venus's-flytrap (*Dionaea muscipula*) (Figs. 35, B; 36, A) accomplish the same object by unique trapping devices. The more or less circular leaf of the sundew is covered with long glandular hairs or "tentacles," at the tips of which is secreted a sticky substance which holds small insects that alight on it. The tentacles then all bend over toward the center of the leaf and hold the insect fast. The outer ends of the leaves of the Venus's-flytrap resemble somewhat a springtrap. Along the outer margin of each half of the leaf blade there is a row of stout teeth, and in the center of each half, on the upper surface, there are three sensitive hairs. When an insect alights on the leaf and touches the sensitive hairs, the two halves of the leaf spring together, folding along the midrib, and hold the insect fast. In both of these plants the digestion of the tissues of the insect and the absorption of the digested products by the leaf proceed apparently as in the pitcher plants.

CHAPTER 6

ROOTS

GENERAL FEATURES

Distinguishing Features. The root is the part of the plant body which ordinarily grows downward into the soil, anchoring the plant and absorbing water and inorganic salts in solution. Yet roots are not necessarily underground structures. The "prop roots" of corn and the "air roots" of orchids are examples of true roots that normally remain partly or wholly above-ground. On the other hand, some recognized stem structures such as tubers and rhizomes normally grow underground. These exceptions emphasize the fact that roots cannot be distinguished from stems on the basis of their position with respect to the soil. Such distinction is based rather upon external and internal structural differences. Unlike stems, roots do not bear leaves and regular buds and hence are not divided into nodes and internodes. For this reason, roots usually branch in an irregular manner. Roots do, however, under certain conditions, develop adventitious buds which give rise to leafy shoots. Such shoots are produced very irregularly and often in profusion when the roots of plants like poplars, black locust, Osage orange, and apple are exposed or are near the surface of the ground. The basis on which roots are differentiated from stems will be better understood after the external and internal structures of these organs have been studied. It may be mentioned here, however, that the presence of a protective structure over the end of the root, known as the rootcap, is distinctly a root characteristic found on no other part of the plant. The arrangement of the internal tissues of the young root is also an important distinguishing feature of roots.

Kinds of Roots. As to size and order of development, roots can be classified as **primary roots**, **secondary roots**, and **adventitious roots**. They may also be classified as **taproots**, **fibrous roots**, and **fleshy roots**.

Primary and Secondary Roots. The root that is first put out by a germinating seed usually grows directly downward and is known as the **primary root** (Fig. 42). The branches from this primary root are called **secondary roots**. Secondary roots originate much farther back from the root apex than do secondary stems (*i.e.*, stem branches) from the stem apex. They also arise from deeper lying tissues, taking their origin from within the vascular cylinder, in a parenchyma tissue called the

pericycle (Figs. 37, 38) which surrounds the central woody region of the root. Here a region of growth is initiated which develops into a young

root tip with its point directed outward. This young branch root or secondary root forces its way through the surrounding cortical tissues and thus reaches and penetrates the soil.

Adventitious Roots. Many grass stems root at the nodes or joints if the stems become prostrate; cut stems of such herbaceous plants as geranium, coleus, and carnation, and one-year-old stems of willow (Fig. 39, A), poplar, and rose will develop roots if placed in moist sand or in water, and even the leaves of such plants as *Begonia* and *Bryophyllum* (Fig. 33) will, in a like manner, "strike root" under suitable conditions. All roots so developed are to be classed as **adventitious roots**. In the cereals, adventitious roots developed at the junction of the root with the stem of the seedling and sometimes at the first nodes of the stem become the principal roots of the plant.

Taproots, Fibrous Roots, and Fleshy Roots.

If the primary root remains the largest root of the plant and continues its growth in a downward direction, so as to become the main root, with all other roots of the plant branching off from it, it is known as a **taproot** (Fig. 39, C). Ragweeds, burdock, dandelions, and oak and hickory trees have well-developed taproots. Monocotyledonous plants usually do not develop taproots. When numerous long, slender roots of about equal size are developed, they are known as **fibrous roots** (Fig. 39, B). In this case, no one root is the largest. Many grasses, plantain, and other plants have fibrous roots. In some plants, like beets (Fig. 40, A), radishes, and turnips, the roots become very large through the storage of food. Such roots are called **fleshy roots** and in most cases are taproots. In other plants, like the *Dahlia* and the sweet potato, several of the roots become fleshy. Such roots are sometimes called **clustered roots** (Fig. 40, B).

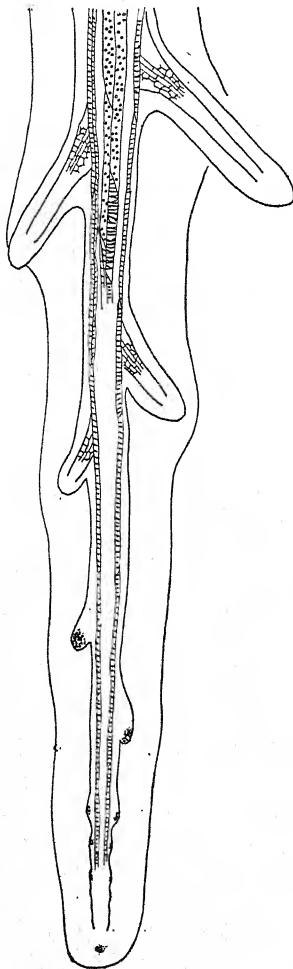


FIG. 37. Diagrammatic representation of origin of secondary roots in water lettuce (*Pistia* sp.); branches toward top are older and show slight differentiation of cells which will lead to development of conducting tissues; cortex of main root broken at older branches; vascular elements indicating spiral thickenings near tip, gradually showing scalariform and pitted condition in older region.

Direction and Extent of Growth of Roots. Recent studies have shown that the extent of root development of common plants is much greater than former knowledge seemed to indicate. In many cases the roots are

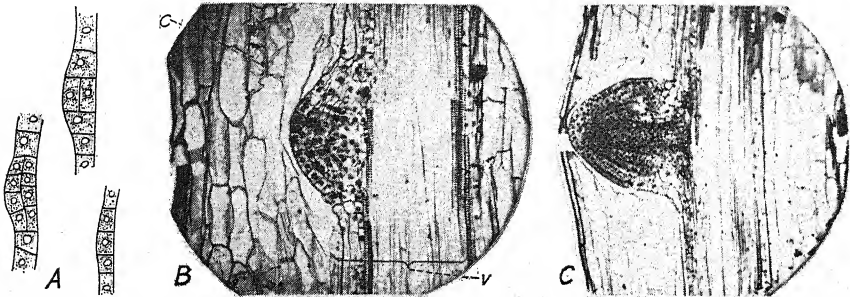


FIG. 38. Successive stages in the development of a secondary root. A, origin of secondary root primordium in the pericycle of the primary root; B, C, development of the young root tip, as it forces its way through the surrounding cortical tissue of the primary root; c, cortex tissues; v, vascular cylinder.

actually much longer, more extensive, and greater in weight than the tops of the same plant (Fig. 41). A single corn-root system, for example, has been found to occupy thoroughly 230 cu. ft. of soil and the roots when placed end to end to have a total length of 1,320 ft. Many different factors influence the direction and extent of growth of roots. The species



FIG. 39. A, willow cutting, showing development of adventitious roots from the stem; B, fibrous roots of the broad-leaved plantain (*Plantago major*); C, a young ragweed plant showing a taproot. (Drawings by Elsie M. McDougle.)

of plant in itself is important. All other influences being alike, one would not expect the root system of an oak tree to resemble that of a bean plant, or that of a dandelion to resemble that of corn. Many of our common Middle Western plants have root systems penetrating to a depth of 3 or 4 ft. Yet alfalfa, growing under similar conditions, has been found in some cases to have roots extending to a depth of 31 ft.

Numerous external or environmental factors are effective in determining the direction and extent of growth. These include gravity, light, temperature, soil texture, soil minerals and salts, oxygen supply, and moisture. Every root is subjected to all of these factors simultaneously and the actual growth made is the resultant of the combined action of all of them.

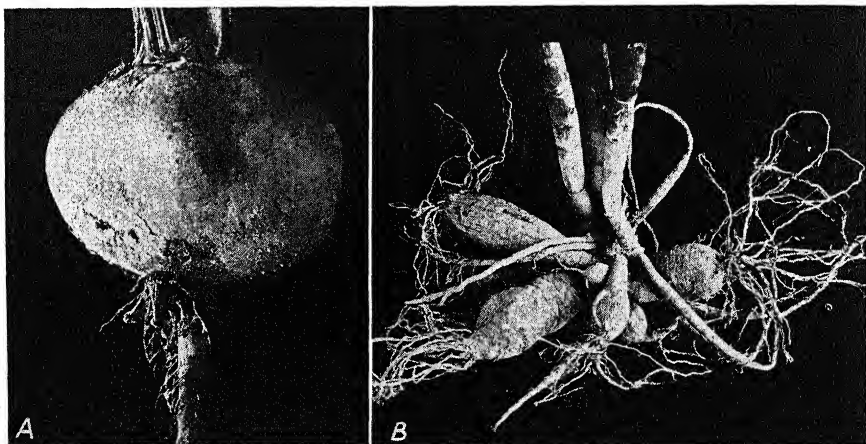


FIG. 40. A, fleshy taproot of the beet; B, clustered roots of *Dahlia*.

In response to gravity, roots in general tend to grow downward. This phenomenon is known as **positive geotropism** (Fig. 104). Some roots, if subjected to one-sided illumination, grow away from the light and exhibit what is known as **negative phototropism**. The majority, however, seem to be indifferent to light as far as direction of growth is concerned. Light indirectly affects the extent of root systems by supplying the tops with energy for photosynthesis. Thus food is manufactured which is transferred to the roots and utilized by them in making further growth. Roots will bend in the direction of the temperature most favorable to their growth, thus exhibiting **positive thermotropism**. Roots develop best in a loose soil and better in a fertilized soil than in a poor one. Nitrogen and phosphorus-containing fertilizers seem to stimulate root development. Since we usually fertilize only the upper soil layers we induce greater root development there, which may be disadvantageous in case of a long dry period.

Oxygen must be available for the respiration of roots, which in turn is

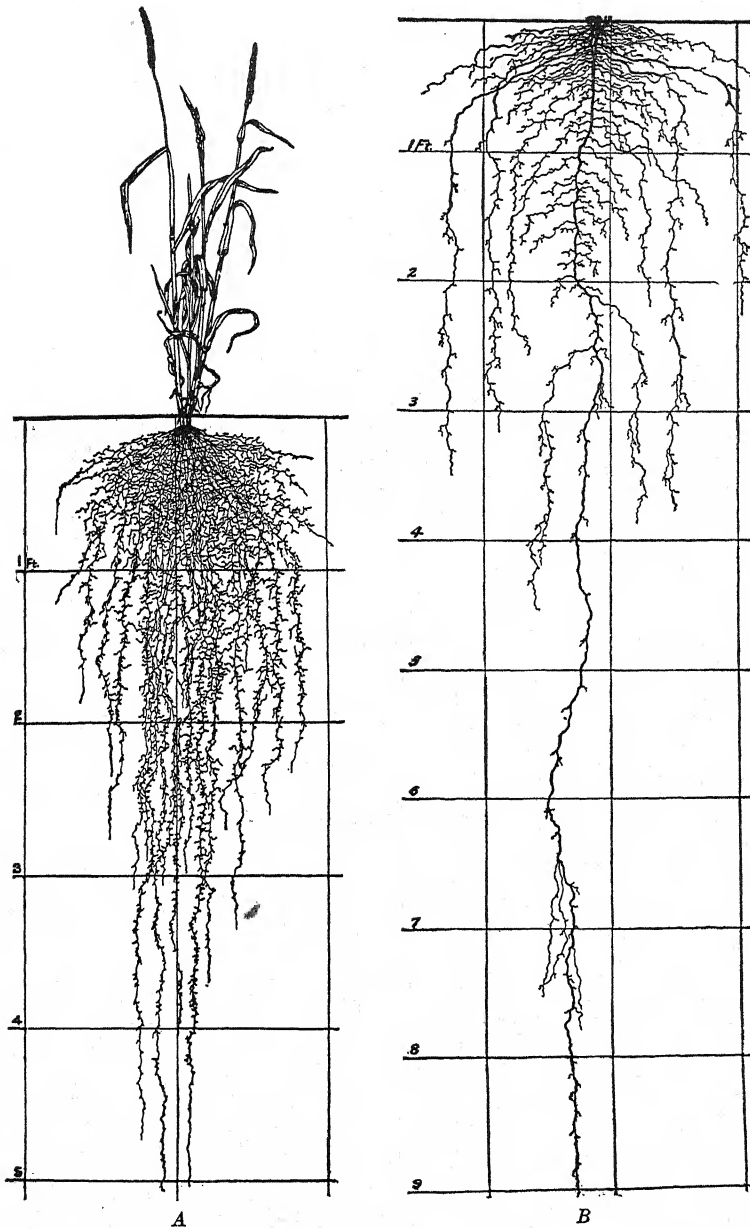


FIG. 41. A, fibrous root system of wheat; B, taproot system of red clover; numbers indicate depth of soil in feet. (From J. E. Weaver, "Root Development of Field Crops," McGraw-Hill Book Company, Inc., New York, 1926.)

necessary in order that growth may occur. Experiments on numerous plants have shown that growth ceases when oxygen is removed by replacing it either with another gas or with water. The amount of oxygen necessary for growth varies with the species. Thus it has been found that the growth of cactus roots is checked when the supply of oxygen is reduced to 12 to 15 per cent, but mesquite roots continue growth when the oxygen content of the air about them is only 2 per cent. Roots at great depths or in waterlogged soils or in very compact soils are likely to suffer from lack of oxygen.

EXTENT OF ROOT SYSTEMS¹

Plant	Maximum		Type of root system	Soil and locality
	Depth, feet	Spread, feet		
Big bluestem grass	9	1	Fibrous ✓	Prairies
Wild rye.....	2 to 3	1.5 to 2	Fibrous ✓	Prairies
Rosinweed.....	9 to 14	3 to 4	Tap	Prairies
Spring wheat.....	4.8	1	Fibrous	Silt loam, Nebraska
Corn.....	8	4	Fibrous	Loess, Nebraska
Alfalfa.....	10 to 20	Tap	Silt loam, Nebraska
Potato.....	2 to 4.7	1 to 2	Fibrous	Loess, Nebraska
Cabbage.....	5	3.5	Fibrous	Nebraska
Strawberry.....	3	1	Fibrous	Silt loam, Nebraska
Pea.....	3 to 3.2	2	Fibrous	
Pumpkin.....	6	5 to 17.5	Tap and fibrous	Nebraska
Tomato.....	3	3 to 4	Fibrous	Ithaca, N. Y.

¹ Data from J. E. Weaver, "Root Development of Field Crops," McGraw-Hill, New York, 1926, and J. E. Weaver and W. E. Bruner, "Root Development of Vegetable Crops," McGraw-Hill, New York, 1927.

Roots do not seek water but will continue to grow in the direction of moisture supply. They are, therefore, **positively hydrotropic**. Moisture is an important factor in determining direction, depth of penetration, and lateral spread of roots. In general, the less the rainfall, the less the penetration and the greater the lateral spread of roots. Conversely, where rainfall is great and where much of the rain penetrates into the soil and the water table is low, the longest and most deeply penetrating roots are found. In desert regions annual plants seldom penetrate to a depth of more than 8 in. with greatest development in the upper 2 or 3 in. In the semiarid regions of the Western plains, Spanish bayonet plants have been found to have roots only 18 in. deep but with a lateral spread of 30 ft. and more. The depth of penetration of the average Middle Western plants has already been given as from 3 to 4 ft. The table shown above gives further information concerning root systems of different kinds of plants.

STRUCTURE OF ROOTS

Root Hairs. Several external features that distinguish roots from stems, such as the absence of leaves, regular buds, nodes, and internodes in the root, have already been pointed out. The external features of young roots can best be observed on seedlings. When seeds are germinated, the first structure to emerge is the root. Roots of this kind are usually white or colorless cylindrical organs more or less rounded off or pointed at the apex (Fig. 42). The apex itself is covered with a thimble-like tissue known as the **rootcap**.

The Root-hair Zone. Several millimeters behind the rootcap will be found a multitude of fine white hairs radiating outward from all sides of the root (Fig. 42). These are called **root hairs**. The shortest root hairs are nearest the rootcap. Farther back they increase in size until the maximum length is reached. The area covered by these hairs is known as the **root-hair zone**. Beyond this narrow zone no hairs are visible. This is explained by the fact that near the root apex new hairs are continually being produced, while in the older region of the root-hair zone the hairs are dying and disappearing. The root-hair zone is therefore constantly moving forward, keeping pace with the growth of the root apex. Since the root hairs are perhaps the most important structures concerned in absorption, it is necessary to consider them in further detail.

Structure of Root Hairs. When seen under the microscope, the root hairs appear as very delicate, colorless outgrowths. Each hair is in reality an outward prolongation of a portion of an epidermal cell (Figs. 43, 52). The outer walls of the epidermal cells in this region are relatively thin and delicate. Consequently it is possible that the root hairs are formed by a bulging out of the epidermal cells resulting from turgor pressure from within. The outer, delicate walls of the root hair consist partly of pectic materials which are gelatinous in nature and enable the root hair to cling to soil particles and to absorb water and salts in solution. The protoplast of the cell furnishes the living content of the root hair, the nucleus of the cell usually migrating outward into the hair. The cytoplasm of the root hair usually lies next to the wall and acts as a plasma membrane. The central part of the root hair is occupied by a large vacuole or

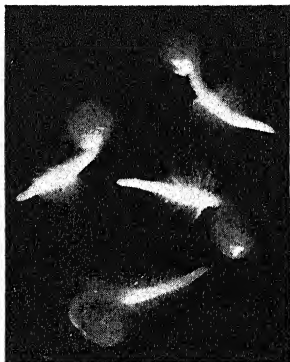


FIG. 42. Seedlings of mustard showing the root-hair zone a short distance back of the root tip of the primary root.

sometimes several vacuoles containing a solution of organic and inorganic salts. Such a structure is admirably suited to absorbing water by osmosis.

Growth and Development of Root Hairs.

Root hairs grow in a direction perpendicular to the surface of the cell from which they arise. In general, they elongate until they come in contact with some solid substance such as a soil particle, against which they flatten out, thus presenting the greatest possible absorbing surface and coming into intimate contact with the film of moisture which surrounds the soil particle. As a result of this response to contact with soil particles, the root hairs assume very irregular forms and cling so tenaciously to the soil particles that it is almost impossible to remove a plant from the soil without leaving behind most of the root hairs. It is chiefly for this reason that plants pulled up out of the soil and transplanted usually wilt unless the transpiring surface is reduced by pruning to compensate for the reduced absorbing surface.

It is not unusual to find 200 to 300 root hairs per square millimeter of epidermis in the root-hair zone. In length they range between 0.1 and 10 mm. and in diameter they average about 0.01 mm. The great numbers of the root hairs and their dimensions cause them to increase the absorbing surface of roots five to eighteen times. The actual size and the intensity of production of root hairs depend upon the conditions under which they are formed. Of these conditions, the kind of plant, the temperature, the moisture, the oxygen supply, and the concentration of various minerals in the soil solution probably are the most important. A slow-growing root usually has a greater density of root hairs per unit area of epidermis than does a fast-growing root. It has long been known that a saturated soil suppresses root-hair development. Some plants like *Anacharis* and *Acorus* fail to develop

root hairs at all when the roots are immersed in water; others, like corn, wheat, squash, and bean, will develop root hairs in water but not

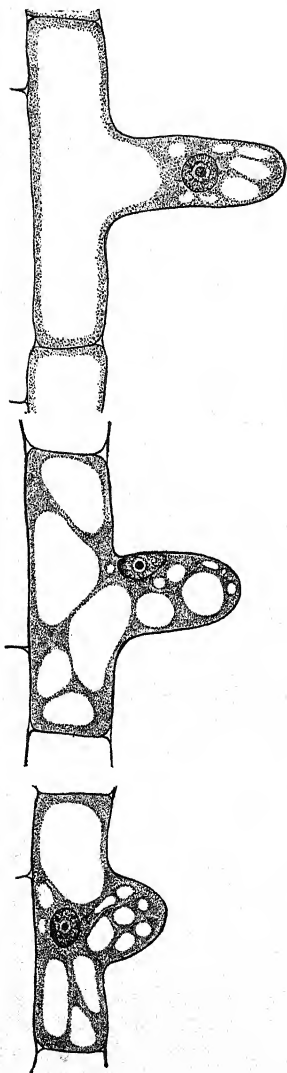


FIG. 43. Root epidermal cells showing development of root hairs. (Drawing by Helen D. Hill.)

so well as when the roots are in a well-aerated soil. A few plants like duckweed and the yellow pond lily develop no root hairs under any conditions. A high concentration of the soil solution suppresses root-hair development. In general, most plants develop root hairs best in a well-aerated, moist soil.

Duration of Root Hairs. Root hairs, as a rule, live for only a few days or at most a few weeks. Exceptions to this have been found in the root hairs of honey locust, Kentucky coffee tree, and redbud. The root hairs of these plants are very thick-walled and persist as long as the root epidermis, which is several months. The root hairs of certain composites have been known to persist for 3 years.

The Regions of the Root. In a lengthwise section of a root several different regions based on the degree of maturity of the cells may be recognized (Figs. 44, 45). These are, in order from the apex toward the base of the root, the **rootcap**, the **zone of cell division**, the **zone of cell enlargement**, the **zone of maturation**, the **zone of primary permanent tissues**, and finally the **zone of secondary tissues**. The root-hair zone begins in the zone of enlargement and extends through the zone of primary permanent tissues, reaching its full development in the latter zone. These various regions or zones of the root are not sharply differentiated but merge gradually into each other.

The Rootcap. The rootcap (Fig. 45) is a distinctive root structure found on practically all roots except those of most aquatic plants, but never found on any other plant organ. It is a loose tissue or a thimble-shaped mass of cells acting as a cap or protective layer for the growing point of the root. It usually originates in one of several different ways. In a few cases it arises from the general meristematic region of the root tip. In some of the dicotyledonous plants it develops from that special meristematic layer that gives rise to the epidermis and is known as the **protoderm** and is therefore definitely related to the epidermis. In the roots of some monocotyledonous plants it arises from a special meristematic region lying just outside the general growing region of the root known as the **calyptragen**. Whatever the method of origin of the rootcap, it is clear that in all cases additions are made to it from certain special tissues of the root itself. These additions replace the outer cells of the root cap that are being continually worn away and sloughed off as the root tip is literally pushed through the soil. The walls of the outer cells of the root cap sometimes become gelatinous and furnish a slimy substance that assists in overcoming friction.

2 *Zone of Cell Division.* Lying under and protected by the rootcap is the active **promeristem**, or **primordial meristem**, of the root (Fig. 45). It is this region which constitutes the zone of cell division. The cells of the promeristem are all alike. They are relatively small parenchyma cells

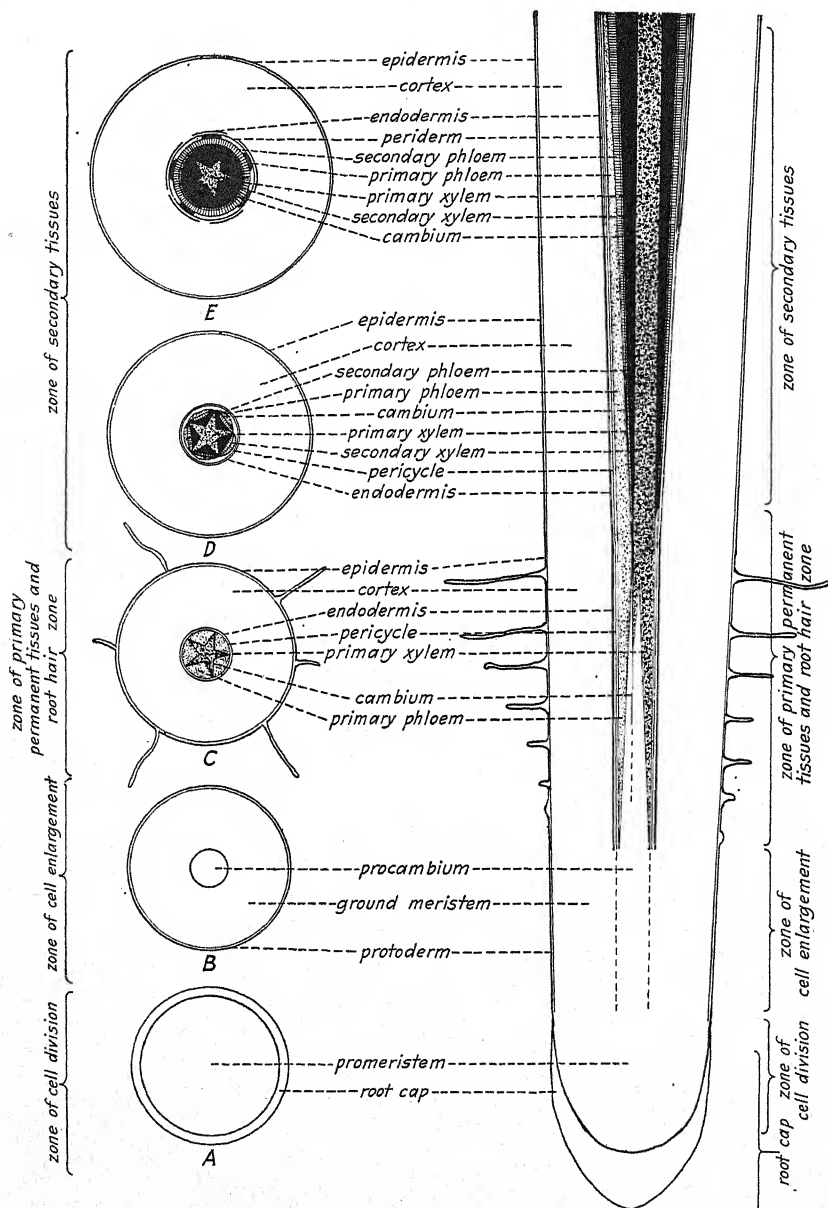


FIG. 44. Diagrammatic representation of the origin and arrangement of primary and secondary tissues in a young root of a dicotyledonous plant; longitudinal section of root at right and transverse sections at different distances from the tip (A-E) at left. Note that the primary xylem is exarch; *i.e.*, the earliest differentiated parts (protoxylem) are nearest the periphery of the stele. (Drawing by F. Brown.)

with rather dense cytoplasm and nuclei that are large in proportion to the size of the cells. The cells are in an active state of division, causing the root to elongate by the addition of new cells. As these new cells are added, they enlarge and the promeristem keeps moving forward, maintaining its position immediately behind the rootcap.

Zone of Cell Enlargement. Directly behind the zone of cell division is the zone of cell enlargement (Fig. 44). It is not sharply separated from the former but in general three distinct regions or tissues can be differentiated, representing the first changes in form of the cells derived from

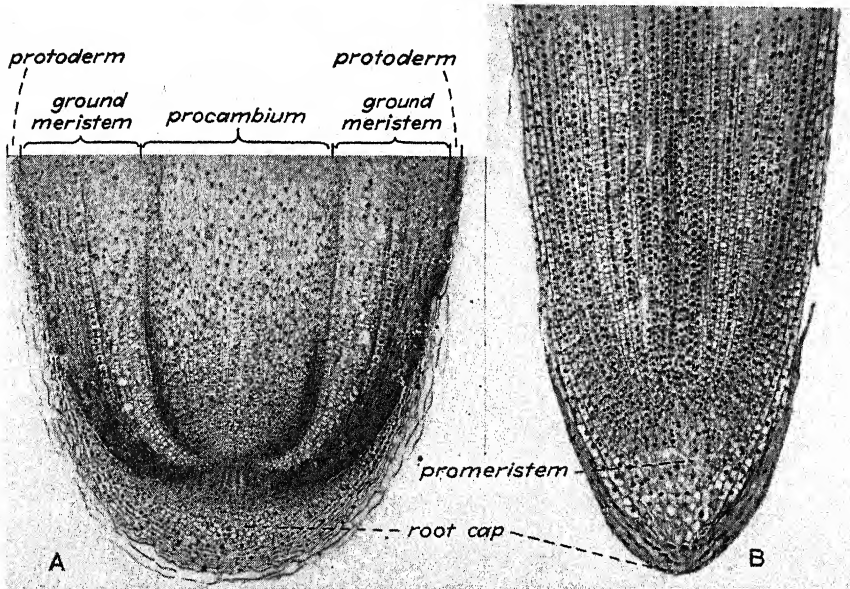


FIG. 45. Longitudinal sections of root tips. A, vanilla; B, onion.

the promeristem (Figs. 44, B; 45, A). These tissues are the protoderm, which later gives rise to the epidermis, the ground meristem, which gives rise to a more or less extensive tissue lying under the epidermis and called the cortex, and the procambium, which gives rise to the central region of the root or vascular cylinder. Since these tissues are all continuing to change in form, they are to be considered as still meristematic and are usually referred to as primary meristems. The zone of cell division, together with the zone of cell enlargement, comprises the actual growing region or zone of elongation of the root. It is worthy of note that this region in roots is short, only a few millimeters (1 to 10 mm.) in length (Fig. 46), as compared with the elongating region of the stem, which is usually several centimeters in length.

Zone of Maturation. As the cells become older, they gradually begin to assume their mature characteristics and thus give rise to the zone of maturation. Here, for the first time, some of the cells are sufficiently differentiated to be recognizable as the permanent tissues they will ultimately become. This is true of the epidermis and of the cortex. Root hairs are developing from the epidermis. In the vascular cylinder, both phloem and xylem are recognizable in part. The first xylem to be differentiated, called **protoxylem**

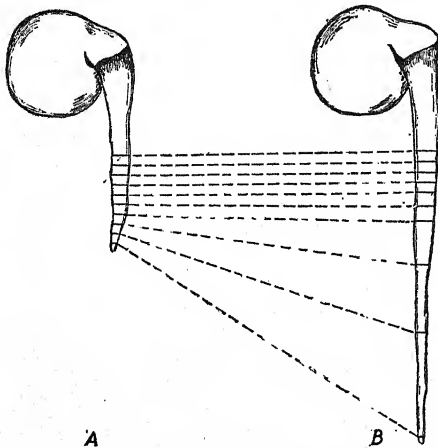


FIG. 46. Growing region of the root. A, a root marked into 1-mm. divisions; B, the same root 24 hr. later. (Drawing by F. Brown.)

(*proto*, first or original), appears in two or more points, on different radii, nearest the outer limits of the central cylinder. The first phloem, called **protophloem**, appears as groups of small cells alternating with the protoxylem cells. The central part of the root remains undifferentiated in the zone of maturation.

Zone of Primary Permanent Tissues. The zone of maturation gradually merges into the zone of primary permanent tissues (Fig. 44, C), so named because the tissues in this zone have reached their permanent form. They are called primary tissues because they are developed directly from the promeristem and are the first permanent tissues to be matured. The primary permanent tissues are described in the following section. It is in this zone of the root that the root hairs reach their full and final development. There is no further increase in length of the root in this or in older regions.

Zone of Secondary Tissues. In dicotyledonous plants and gymnosperms the entire older region of the root beyond the zone of primary permanent tissues constitutes the zone of secondary tissues, so called because in this zone secondary tissues are added to the primary tissues. These secondary tissues are developed by the activity of cambium and cause the root to increase in diameter. They are described later. In the older parts of this zone, the root hairs have ceased to function because of a corky, waterproof secondary tissue which develops in the outer regions of the root. In monocotyledonous plants in general there is no zone of secondary tissues.

The Primary Permanent Tissues. The general anatomical features of a

young root can be studied best from the cross-sectional view (Fig. 44, C; 47 I, A-C, II, A). The primary permanent tissues, derived directly from the primary meristems, consist of **epidermis**, **cortex**, **endodermis**, **pericycle**, **protophloem**, **metaphloem**, **cambium**, **protoxylem**, and **metaxylem**. The central tissues, bounded externally by the endodermis, constitute the **vascular cylinder**.

The **epidermis** is made up usually of a single layer of parenchyma cells constituting the outermost tissue of the root. Many of the cells of the epidermis develop root hairs which, as previously mentioned, are merely epidermal outgrowths. The **cortex** is a rather extensive fundamental tissue lying between the epidermis and the endodermis. It is made up of rather large, many-sided parenchyma cells sometimes nearly rounded and often with many intercellular spaces. The cortex at first functions in the transfer of water and minerals from the root hairs to the xylem but later is chiefly a food-storage tissue. Its cells are often filled with starch grains.

The **endodermis** is a rather conspicuous, well-developed tissue in roots. Usually it consists of a single layer of cells forming the inner boundary of the cortex. When fully differentiated, the cells are often much thicker walled than the cortical cells. In cross section they usually have an oval shape, the radial walls appearing thicker than the tangential walls. The radial and transverse walls of these cells are characterized by the presence of a strip of suberized or lignified material of varying thickness, often running all around the cell, called the **Casparian strip**. The cells of the endodermis opposite the protoxylem points are usually the last to be differentiated, thereby forming a direct passage through the thin tangential walls to the xylem for water and minerals absorbed by the root hairs and transferred through the cortex.

Next to the endodermis and external to the xylem and phloem, forming the outer boundary of the vascular cylinder, is the **pericycle**, consisting of one or more layers of parenchyma cells. Often the pericycle of roots is a single layer of cells. Though not as conspicuous as the endodermis, it is a very important tissue in roots because of the fact that secondary roots originate in the cells of the pericycle and because it gives rise in most cases to the cork cambium or phellogen, to be described later.

The xylem occupies the center of the vascular cylinder and extends outward in two, three, four, five or more star-shaped rays to the pericycle. Depending upon the number of these rays, these conditions of the xylem are referred to as **diarch**, **triarch**, **tetrarch**, **pentarch**, etc., respectively. The first xylem to be matured is the **protoxylem**, constituting the points of the rays. Later the more centrally placed xylem cells are matured, joining these rays and constituting the **metaxylem**. The protoxylem and metaxylem together are the **primary xylem**. In some roots in which

the metaxylem does not differentiate to the very center, as in monocotyledonous plants and gymnosperms, there remains a central region of undifferentiated parenchyma cells (Fig. 47, I, C). This arrangement of the xylem, with the protoxylem external to the metaxylem, is called **exarch** and is characteristic of all roots. The kinds of cells that make up the xylem were described in the chapter on the cell (pages 35 to 36). One of the principal functions of the xylem is the upward transport of water and inorganic substances absorbed from the soil by the roots. This upward transport takes place through tracheids and tracheae, or vessels, both of which have lost their original cell contents and are no longer living, but which carry on their function in an entirely passive and mechanical manner. The xylem also contains wood fibers that function in support and strengthening of the root.

In each of the angles formed by the star-shaped xylem, there is a group of somewhat smaller and thinner walled cells comprising the **primary phloem** tissue. The outer part of this tissue, next to the pericycle, is the first to be fully differentiated and is called the **protophloem**, while the inner part is the **metaphloem**. Protophloem and metaphloem are not as readily distinguishable as are protoxylem and metaxylem. The phloem functions mainly in the transport of manufactured food, which takes place through the sieve tubes already described in the chapter on the cell.

In dicotyledonous plants and gymnosperms the regions of phloem are separated from the regions of xylem by thin-walled, undifferentiated parenchyma cells, one layer of which, retaining its meristematic character, becomes the **vascular cambium** layer, the function of which is later to produce new cells. In a cross-sectional view of the root this cambium seems to lie on and between the arms of the star-shaped xylem, separating it from the phloem. The cambium cells continue to divide and give rise to the secondary tissues of the vascular cylinder. In monocotyledonous plants there is no cambium.

~~The vascular skeleton of a plant is called a stele. The vascular cylinder of a root is known as a radial stele,~~ because of the radial arrangement of the tissues. This radial arrangement of the xylem and phloem is perhaps the most efficient arrangement possible for the accomplishment of the functions of these tissues in roots, as is shown later in the text. The radial stele is characteristic of all roots.

Secondary Tissues; Increase in Diameter of Roots. Increase in the diameter of roots occurs partly by the enlargement of the cells already present and partly by the addition of new cells. Most of the cells that enter into the structure of the older portions of the root have become more or less specialized and no longer divide to produce new cells. Of the primary permanent tissues only the cambium and the pericycle cells

ordinarily continue to divide and it is from them that new tissues are developed. These new tissues are known as secondary tissues. In general, **primary tissues** are those derived directly from the primary meristems, while **secondary tissues** are those derived from the activities of cambium or from living tissues which were already fully differentiated. In general, there are two principal types of secondary tissues developed in the roots of dicotyledonous plants and gymnosperms, viz., **secondary tissues in the vascular cylinder** and the **periderm**.

Secondary Tissues in the Vascular Cylinder. Of all the cells of the primary permanent tissues, the vascular cambium cells alone remain in the meristematic condition and thus continue to divide. The vascular cambium lies between the phloem and the xylem, and by the division of its cells, new cells are added to both the phloem and the xylem. Consequently both of these tissues increase in size, but the latter grows much more rapidly than the former and eventually fills out the sections between the radiating arms of xylem originally occupied by the primary phloem (Figs. 44; 47, I, D-E; II, B). This pushes the phloem cells outward until eventually the xylem region becomes a regular cylinder, circular in cross section. After this stage has been reached, the radial symmetry of the stele has been destroyed, and roots of this age can be distinguished from stems, in cross-sectional view, only in so far as the earlier, primary xylem remains recognizable. The cambium becomes completely continuous in this development, visible in the cross section of the root as a continuous layer of cells between xylem and phloem. Likewise the phloem, previously occurring only as groups of cells between the radiating arms of xylem, now also becomes a continuous cylinder of tissue external to the xylem. All the tissues external to the phloem are forced outward by this development. Since this increase occurs yearly in perennial roots, it follows that each year there is laid down a certain amount of new xylem or wood tissue, and the root comes to have in cross-section the same evident annual rings characteristic of woody stems.

Monocotyledonous plants, lacking a cambium, have no true secondary growth of this type, and in general the root structure of monocotyledonous plants is quite different from that of dicotyledonous plants and gymnosperms. Most of the increase in diameter of roots of monocotyledonous plants takes place by the enlargement of cells of the primary permanent tissues, but in a few kinds of more or less woody species there is a special type of secondary thickening.

The Periderm. In many roots, while the central cylinder is growing in diameter by the addition of secondary tissues, a new secondary tissue arises usually in the pericycle. The cells of the pericycle begin to divide, and when they do, the pericycle is transformed into a new cambium known

as the **phellogen**, or **cork cambium**. The phellogen usually remains as a single layer of cells, and new layers of cells are added both outwardly and

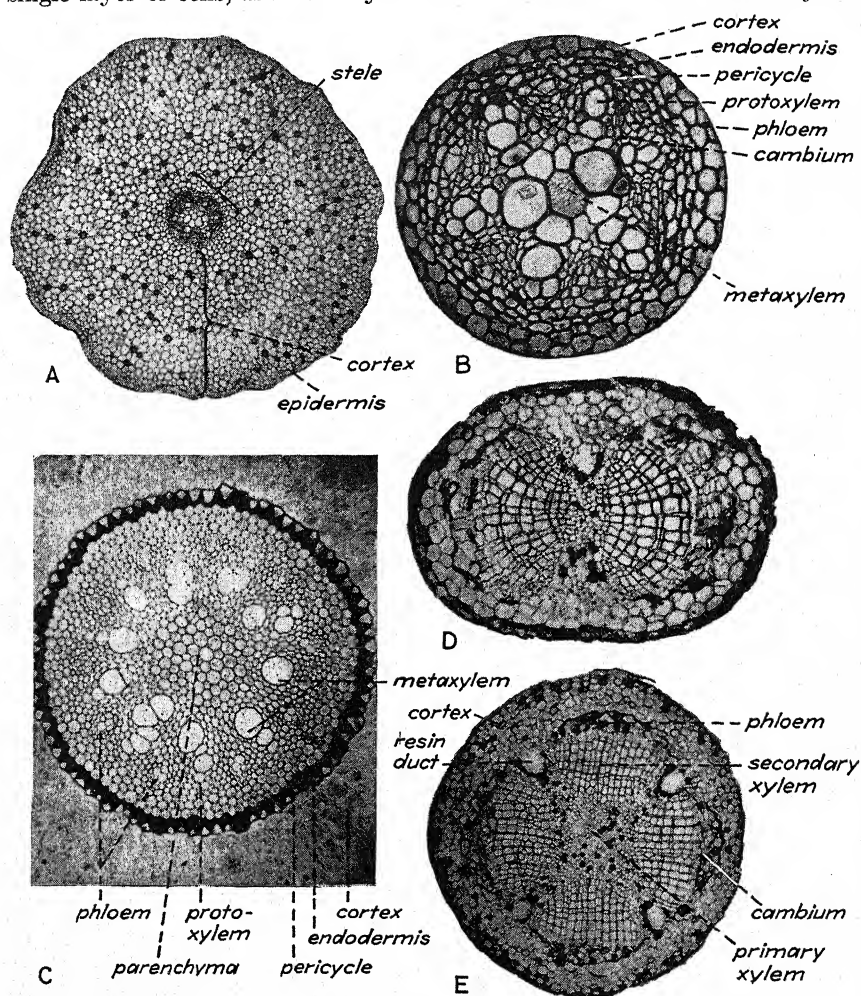


FIG. 47. I. Transverse sections of roots. A, entire section of root of *Ranunculus*, showing primary permanent tissues; B, enlarged stelar portion of A; C, stelar portion of a young root of *Smilax*, a monocotyledon, showing a central region of undifferentiated parenchyma together with the usual primary permanent tissues; D and E, cross sections of pine roots showing secondary tissues; D, diarch; E, tetrarch.

inwardly by its divisions. Those developed outwardly, next to the endodermis and cortex, constitute the **phellem**, or **cork**. Those developed inwardly, next to the phloem, are called **phelloderm**, and the entire new tissue made up of phellem, phellogen, and phelloderm is called the **peri-**

derm (Fig. 47, II, B). The cells of the phelloderm are parenchyma and remain alive and active. The cells of the phellem become suberized,

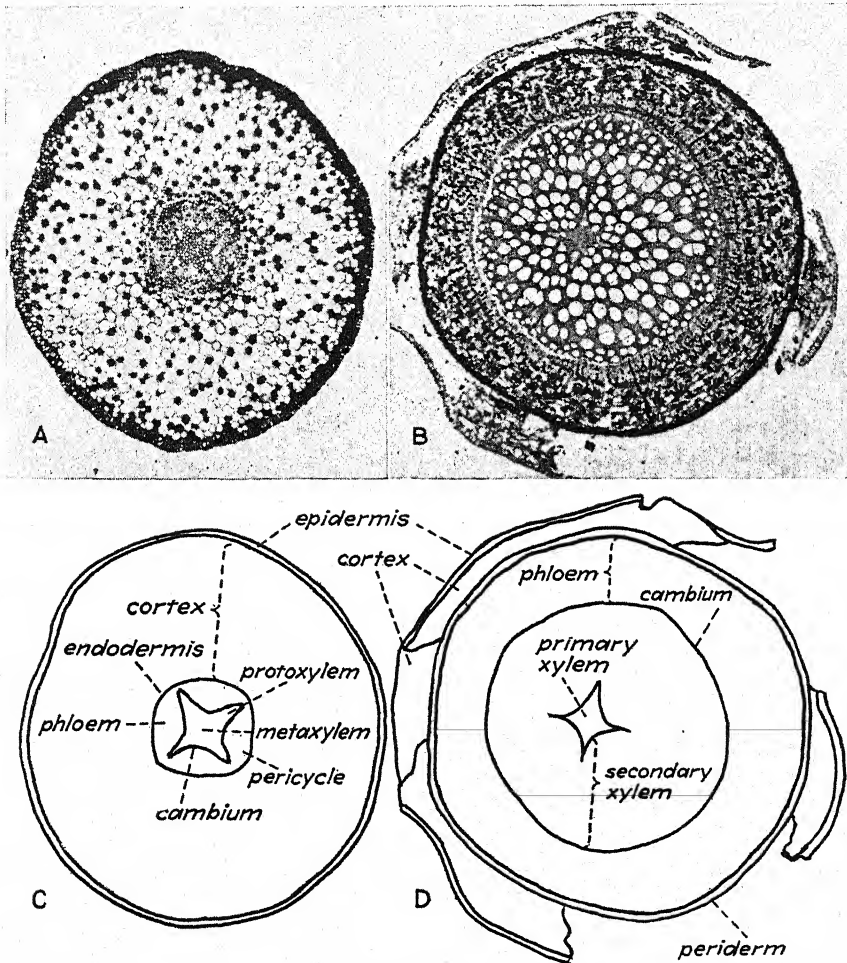


FIG. 47, II. Photomicrographs of transverse sections of *Salix* roots. A, young root greatly magnified showing only primary permanent tissues; B, root one year old, less highly magnified than A, showing secondary tissues. Endodermis, cortex, and epidermis are torn as a result of internal expansion, the endodermis being no longer discernible. C and D, diagrams of A and B, respectively, indicating tissues. (Photomicrographs by D. A. Kribs.)

thus rendering them virtually waterproof, and at maturity they die, forming a rather impervious, protective layer around the outside of the root. Usually in roots there is relatively more phelloderm tissue developed than cork. When the periderm is fully developed, the epidermis,

with its root hairs, and the cortex die and are gradually lost, so that in old roots the periderm becomes the outermost tissue. Obviously the absorption of water and minerals by old roots of this type is reduced to a minimum. As the root keeps growing in diameter, new periderm layers develop in the phloem tissue and the outer layers become broken up and furrowed as does the bark of the stems of trees. The outer dead tissues of the root, however, being underground, often decay.

FUNCTION OF ROOTS

Roots are used by different kinds of plants in many different ways, but common to most roots are the functions of **absorption, conduction, anchorage, and storage**. In many plants, roots may also serve as **asexual reproductive structures**.

Absorption and Conduction. Perhaps the most important function of roots is that of absorption of water and inorganic salts. Since the higher plants grow almost exclusively on land, it is necessary for them to be in direct contact with the supply of water and inorganic salts that exists in the soil. The problem of obtaining these materials has been taken over in such plants by the roots. The manner in which roots obtain these materials is taken up in the following chapter. It is interesting to note here, however, that only the youngest roots of the plant are ordinarily concerned in absorption. As a rule, most of the water and minerals the plant obtains are taken in by roots only a few weeks or at most a year old, regardless of how old the plant may be. Thus even the oldest trees must constantly develop new roots if absorption is to continue.

Once these materials are absorbed from the soil, the root also serves to pass them on to the stem. The xylem of the root is continuous with that of the stem and by this means water and inorganic salts can be distributed throughout the plant.

Anchorage. While it is important to have a part of the plant in contact with the supply of water and inorganic salts, it is likewise important to have other parts so placed as to enable them to receive light and air. This is accomplished in many plants by upright stems and spreading branches. Roots serve to support the stem by anchoring it to the soil. It is obvious that a deep-rooted plant can serve this purpose better than a shallow-rooted one. Thus taprooted trees are not so readily wind-thrown as are surface-rooted forms.

Storage. In most plants, part of the food manufactured in the parts aboveground is carried to the roots and stored there for future use. Such storage of food is particularly found in biennial and perennial plants in temperate regions. Biennials like the beet, mullein, and cabbage usually develop a rosette of leaves during the first year of their growth. During

this year large amounts of food are made and stored in the roots. The following year these stored reserves are drawn on to develop an upright shoot on which flowers and seed are produced, after which the plant dies.

Very often roots become large and fleshy as the result of food storage. This is true of sweet potatoes, radishes, beets, turnips, and many others. The internal structure of such roots becomes highly modified to accommodate the stored reserves. Many of these plants are of considerable economic importance.

The roots of many desert plants also store water, a fact which partly explains their ability to live under arid conditions.

Reproduction by Means of Roots. Since many roots are capable of developing adventitious buds which give rise to leafy shoots, roots are sometimes a means of propagating plants. While the number of instances in which this feature occurs in nature may be limited, it is made use of by man in propagating many forms that otherwise might be difficult to propagate. Thus sweet potatoes are regularly grown from root cuttings much as the white potato is grown from tuber (stem) cuttings. Some plants when cut down to the roots, develop adventitious buds which give rise to new plants. This is sometimes made use of in the propagation of roses and other plants. When the roots of some plants, for some reason or other, become exposed to light, adventitious buds often arise which give rise to new plants. This is true of poplars, apples, black locust, and others.

ROOTS OF UNUSUAL FORM OR FUNCTION

The functions of roots thus far considered are those that are more or less common to most roots. There are plants, however, in which at least some of the roots have become so highly specialized in the performance of some one function as completely to change their structure. This function may be one of those ordinarily performed by roots or it may be one entirely different. In either case such specialized roots may be greatly modified in form and appearance.

Storage Roots. An example of root modification has already been given in connection with food storage in roots. While food storage is a normal function of all roots, in some it has been carried to such a point as to alter completely the appearance as well as the internal structure of the root. In the beet, for instance, successive cambium layers or rings are formed outside the original one. These rings give rise to xylem, phloem, and broad bands of parenchyma tissue which gradually become filled with carbohydrates as the root grows. The root thus becomes unusually large and fleshy. The best examples of such fleshy storage roots are found among taprooted plants of which the carrot, the turnip, and the radish are common examples (Fig. 48, A-C). Many wild plants also

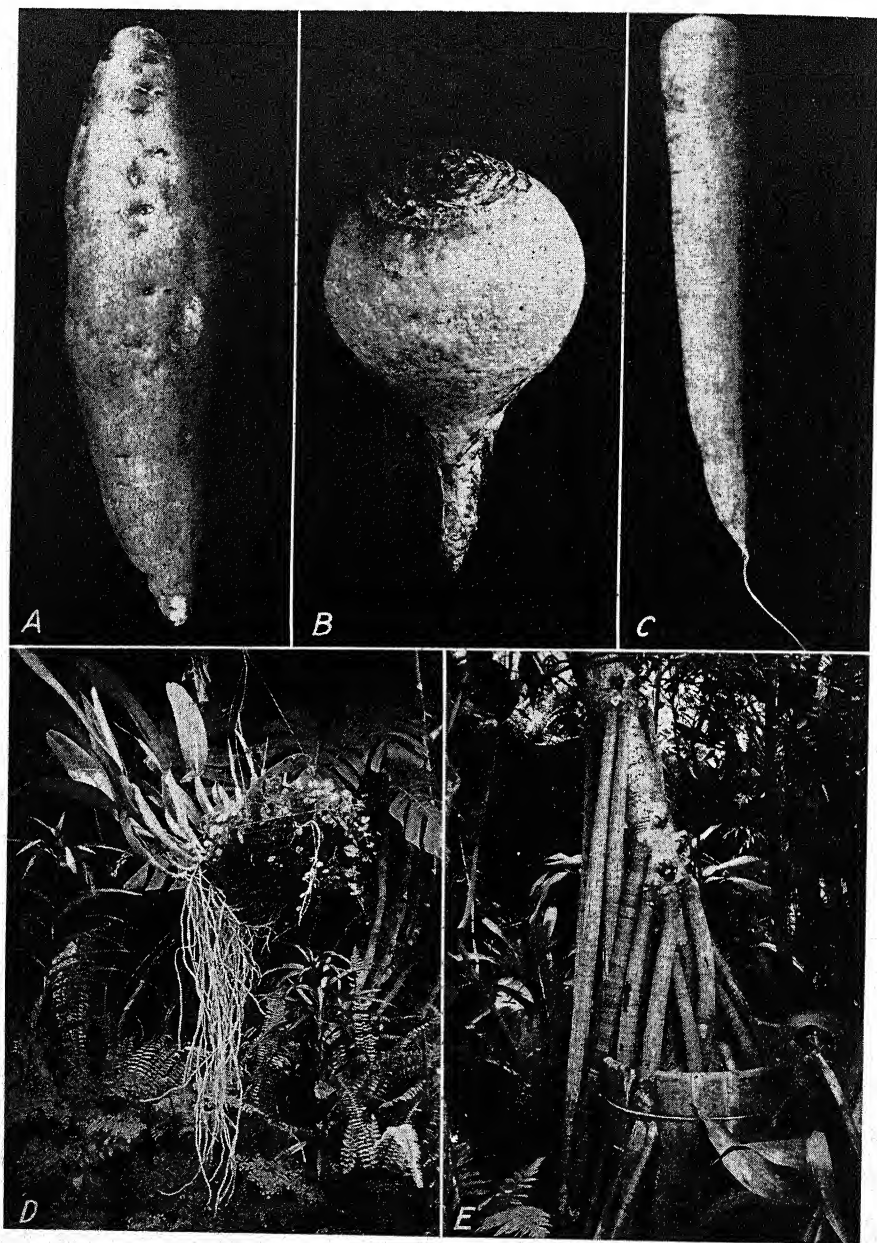


FIG. 48. Roots of various forms or functions. A-C, food-storage roots; A, sweet potato, one of a group of clustered roots; B, turnip, taproot; C, carrot, taproot; D, aerial roots of a tropical epiphytic orchid; E, prop roots of the screw pine (*Pandanus* sp.).

have fleshy storage roots of this type, which admirably enable them to live over winter in a resting condition and to start renewed growth in the spring by utilizing the large stores of reserve food. Dandelion and burdock have roots of this type. In some plants, several of the roots become fleshy. These have already been referred to as clustered roots. Dahlia (Fig. 40, *B*), the rue anemone, and the sweet potato (Fig. 48, *A*) have clustered roots. In the sweet potato some of the adventitious roots developed at the nodes of stems lying on the ground become fleshy.

Aerial Roots. While roots are normally underground structures, in certain species of plants they are found partly or entirely above-ground. These are spoken of as aerial roots. When the stems of corn have begun to grow rapidly, the first few nodes above the soil send down a cluster of aerial, stilt-like roots to the soil. These roots help to support the tall columnar stem but they also grow into the ground and function in absorption of water and inorganic salts. Such roots are also found in the screw pine (*Pandanus*) and in other species. Roots of this type are sometimes called **prop roots** (Fig. 48, *E*).

The mangrove tree, which grows along sea-shores in the tropics, sends down roots from its branches to the water beneath. These roots, formed in great numbers, catch sand and drift which causes the space to be filled up to form soil. For this reason the tree is often said to "march into the sea." The banyan tree of India also sends down roots from its branches. These roots send up shoots by means of which a single tree may soon develop into a grove of trees.

The best examples of aerial or air roots are found among some of the tropical orchids (Fig. 48, *D*). These plants are **epiphytes**; *i.e.*, they rest upon the trunks of trees or other supports and absorb water and minerals directly from rain as it falls on the aerial roots. These roots remain permanently in the air. They have a spongelike tissue near the exterior, called the **velamen**, which enables them to absorb and hold water. In many of these plants the roots develop chlorophyll and carry on photosynthesis, a very unusual function for roots.

The **climbing roots** of such plants as the trumpet creeper, English ivy,

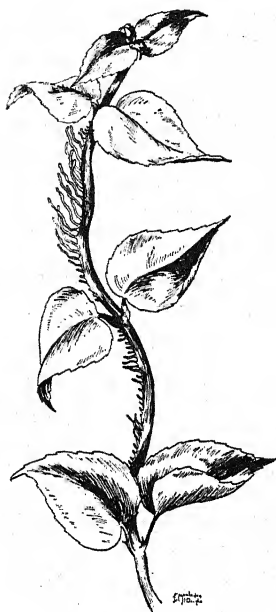


FIG. 49. Climbing roots of the climbing *Hydrangea*. (Drawn by Elsie M. McDougale.)

poison ivy, and climbing hydrangea (Fig. 49) are also a form of aerial root. Large numbers of these roots are usually formed on the sides of stems growing along a wall or other support where they flatten out and hold the stem firmly to the surface. In some of the tropical climbers (*Ficus*) these roots become very long and sometimes grow around supports like tendrils.

Roots of Parasitic Plants. A highly modified type of root is found in such parasites as mistletoe and the common dodder. The seeds of mistletoe germinate on the branches of trees and send their roots into the tissues from which water and minerals and possibly food are absorbed. The common dodder (Fig. 34, *B*) is a parasitic twiner which sends out roots into the stem of the host plant wherever it comes in contact with it. These roots, called **haustoria**, penetrate to the vascular bundles and absorb nourishment from them. Dodder is sometimes a serious pest on clover. The leaves of mistletoe are green and carry on photosynthesis, but dodder depends almost entirely upon the host plant for its food.

Other Modified Roots. Other modifications of roots occur in water plants. It is not unusual to find in the roots of such plants large air spaces for facilitating gaseous exchange and for conducting air to the submerged parts. The internal anatomy of roots of this type is greatly altered.

The Spanish moss (*Tillandsia*), a characteristic plant of the South, found hanging in masses from trees and often from telephone lines, has no roots at all. It is an epiphyte in which the ordinary functions of the root have been taken over by other parts of the plant.

CHAPTER 7

ABSORPTION OF WATER AND INORGANIC SALTS

IMPORTANCE OF WATER AND INORGANIC SALTS

Of the various materials the plant gets from its environment none is more important than water. The very composition of plants attests this, most herbaceous plants being made up of 70 to 85 per cent water and even woody parts of plants consisting of as much as 50 per cent water. Algae and other water plants frequently contain 95 to 98 per cent water. Moreover, plants growing in soil are constantly losing large quantities of water by transpiration. This water must be supplied through absorption by the roots if wilting of the plant is to be prevented. Water, being the most important solvent in nature, is the medium by which inorganic salts and elaborated foods are transported from one part of the plant to another. Without a constant supply of water the plant could not carry on any of its physiological activities such as photosynthesis, digestion, respiration, and growth.

Obviously a knowledge of the manner in which plants get water is important. It is no less important to know how inorganic salts are obtained since they are the raw materials out of which many of the constituents of plants are made. In the following paragraphs these matters are considered.

PRINCIPLES UNDERLYING ABSORPTION

Imbibition. When a piece of hard, dry gelatin is dropped into a tumbler of water, it immediately absorbs the water, thereby becoming soft and pliable. So long as the water is not heated the gelatin will maintain its general shape although it will have swollen to many times its original size. This swelling of an apparently homogeneous, pore-free substance is called **imbibition**. The swelling is thought to be caused by the entering of water molecules between the particles of the gelatin itself, which will separate only to a definite limit determined by a balance between the attraction of the particles for each other and their attraction for water. The solid particles of gelatin in this case are thought to be groups of molecules or colloid particles, or the gelatin is said to be a **hydrophilic colloid** because of its affinity for water, the term "hydrophilic" meaning simply water loving. The root hairs of plants likewise consist largely of hydrophilic colloids which enable them to soak up water much as gelatin does.

Although we are dealing here with absorption of water by roots, it should be mentioned that imbibition is important to the plant in many other ways also. Practically all parts of the plant, except the external waterproofed layers, contain hydrophilic colloids. Not only do such parts of the plant imbibe water but they hold some of this water with considerable force. Water held in this manner is referred to as "bound water." The amount of bound water in a plant has much to do with the ability of the plant to withstand drying as well as freezing. Thus desert plants usually develop hydrophilic colloids which enable them to conserve water and live under conditions which would quickly kill other plants. The same may be said of winter-hardy plants. Hardy varieties are usually those that develop hydrophilic colloids which are able to bind some of the water so as to prevent freezing injury.

Imbibition also plays a part in the transfer and distribution of water in the plant, in the ascent of sap, in the general physical part of protoplasmic activity, in plant growth, and in many plant movements.

Diffusion of Gases. According to the kinetic theory, the ultimate particles of all substances are in a constant state of motion. When a gas, therefore, is liberated in a room, the molecules of the gas, by virtue of their own kinetic energy, spread abroad until they become evenly distributed throughout the room. This spreading abroad is called **diffusion**. Since there are more particles moving in a region of high concentration of a gas, it is obvious that diffusion will be more rapid from a region of high concentration toward a region of low concentration than in the reverse direction. When two or more gases are brought together, they will intermingle completely. In this case, the direction of diffusion of each gas is not influenced by the presence of or direction of diffusion of the other gases, but each one will diffuse more rapidly from a region of high concentration of that particular gas, regardless of what the direction of diffusion of the other gases may be. For example, as a result of the liberation of oxygen in photosynthesis, the concentration of this gas tends to become higher inside the leaf than it is in the surrounding atmosphere. Consequently more oxygen moves out of the leaf than moves in. At the same time carbon dioxide is being consumed in photosynthesis. The concentration of carbon dioxide therefore tends to be greater outside the leaf than inside and therefore more of it moves into the leaf than moves out. Here then we have oxygen gas moving more rapidly outward at the same time that carbon dioxide is moving more rapidly inward. At night, of course, the reverse is true. While the *direction* of diffusion is thus not influenced by other gases, the *rate* of diffusion is influenced. Any gas will diffuse more rapidly into a vacuum than it will into any other gas or mixture of gases. The greater the combined concentration of other gases,

the slower will be the rate of diffusion of a particular gas into the other gases. Furthermore, not all substances diffuse at the same rate under the same conditions. For instance, hydrogen gas, having a density of 1, moves four times as rapidly as oxygen, the density of which is 16. In other words, the rate of diffusion of a particular gas is inversely proportional to the square root of its density. The rate of diffusion is also influenced by temperature, being directly proportional to the absolute temperature or increasing $\frac{1}{273}$ for every degree rise in temperature above 0°C . The higher temperature imparts greater energy to the diffusing particles and therefore increases the velocity.

Summarizing, we can say that the rate of diffusion of a gas depends upon the concentration of the gas, the temperature, the density, and the presence of other gases. The actual rate therefore will be the resultant of the combined action of all of these factors.

Diffusion of Dissolved Substances. If a solid, liquid, or gas is introduced into a liquid in which it dissolves, it will behave like a gas diffusing in air; *i.e.*, the molecules or ions of the substance will in time become equally distributed throughout the liquid. Thus a little sugar dropped to the bottom of a tumbler of water will soon dissolve and the molecules will diffuse through the water even though it is not stirred. The dissolved substance in this case is called the **solute**, the liquid in which it is dissolved, the **solvent**, and the whole system is called a **solution**.

A solution may contain many kinds of solutes just as air consists of several gases. Indeed in the soil and in the plant the solutions met with are always made up of many solutes. The rate of diffusion of a solute is determined by the same factors that govern the diffusion of gases; *viz.*, concentration, temperature, density, and the presence of other solutes. In general, the rate of diffusion of a solute is always greater from a region of high concentration of that particular solute to one of lower concentration, regardless of how many other solutes may be present. It cannot be overemphasized here that each solute in a complex solution moves independently of the movement of other solutes. When two or more solutions of different concentrations are brought together, diffusion of all solutes continues until the concentration of each solute becomes equalized throughout the liquid.

Diffusion through Membranes. Both gases and dissolved substances may diffuse through membranes in which the solvent is imbibed. The rate of diffusion in this case is determined by the nature of the membrane as well as by all the other factors that govern the rate of diffusion. Membranes differ greatly in the ease with which solutes and solvents can pass through them. A rubber membrane, for example, allows neither water nor any solutes dissolved in water to pass through it. Such a membrane is

said to be **impermeable**. A filter paper, on the other hand, will allow both water and any substance dissolved in water to pass through it. In this case the membrane is said to be **permeable**. There is a third class of membranes which permits a solvent to pass but may prohibit the passage of many substances in solution. This type of membrane is said to be **semipermeable** or **selectively permeable**. We may characterize the three types of membranes as follows:

1. Impermeable membranes allow neither solvent nor solute to pass.
2. Permeable membranes allow both solvent and solute to pass.
3. Semipermeable or selectively permeable membranes allow the solvent to pass but prohibit the passage of many solutes.

It should be said in connection with semipermeable membranes that no membrane is known to exist which bars the passage of all solutes. A membrane is said to be semipermeable, however, if it prevents the passage of many solutes or if it does not allow solutes to pass as readily as it allows the solvent to pass.

Cell Membranes. In plants all three types of membranes are found. In this connection, the only solvent we need to concern ourselves with is water. Suberized and heavily cutinized cell walls are practically impermeable as regards the passage of water and solutes. Ordinary cellulose cell walls, on the other hand, are readily permeable to both water and the substances dissolved in water. When cell membranes are spoken of, it is usually not the wall of the cell that is meant but the protoplasm lying next to the wall, called the plasma membrane. The protoplasmic membrane of a living cell is selectively permeable. It is this membrane that is most significant in absorption of water and solutes by the cell, since, in the final analysis, it governs the exchange of all materials between the interior and the exterior of the cell. *Perhaps the most interesting feature about the protoplasmic membrane is the fact that its permeability is not fixed and constant but fluctuates.* It may under certain conditions permit a certain substance to pass which under another set of conditions would be prohibited from passing. For instance, the cell sap of root hairs contains sugar which, under ordinary conditions, cannot escape from the root hair because the protoplasmic membrane of the root hair is impermeable to sugar. If, however, the root is immersed in a single salt solution of sodium or potassium, the sugar immediately passes out. In this case a change in the external environment of the root hair has changed the permeability of its protoplasmic membrane. Other factors or conditions bring about similar reversals and changes in the permeability of plant-cell membranes. When a membrane is permeable to a given substance, that substance, so far as is known at present, can pass equally readily through the membrane from either side. That is, if a plant cell permits the passage of a solute from the outside to the interior of the cell, it will

usually also permit its passage from the interior to the exterior. The selective permeability of the protoplasmic membranes is a function of the living cell only. Dead cells are permeable to solutes generally.

Osmosis and Osmotic Pressure. When a *permeable* membrane is placed between a solution and a pure solvent, both the solvent and the solute will diffuse through the membrane until at equilibrium the concentration will be the same on both sides of the membrane. Thus, in Fig. 50, if *a* is a *permeable* membrane and we place water in *A* and a water

solution of sugar in *B*, water molecules will move from *A* to *B* as well as from *B* to *A*. Sugar molecules will also move through the membrane from *B* to *A*. After sugar molecules have passed into *A*, some of them will diffuse back again from *A* to *B*. At the start, more sugar molecules will be moving from *B* to *A* while more water molecules will be moving from *A* to *B*. In other words, each diffusing substance will move faster from a region of high concentration of that substance to a region of lower concentration than vice versa. When equilibrium is reached there

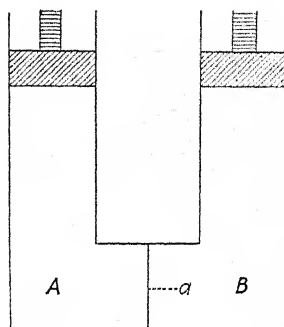


FIG. 50. Explanation in the text.

will be as much sugar in *A* as there is in *B*. Both sugar molecules and water molecules will still continue to diffuse but the level of the liquid on either side of the membrane will not change because at any given moment there will be as many molecules of water and of sugar passing through the membrane from one side as from the other. In other words, diffusion will take place in the same way as it would if no membrane at all were present,

Now suppose that we substitute a *selectively permeable* membrane at *a*, i.e., one that will allow water to pass but not sugar, and again place water in *A* and a sugar solution in *B*. Obviously water molecules will still continue to diffuse through the membrane from both sides but, since there are relatively more water molecules striking the membrane from side *A* than there are from side *B*, water will move more rapidly from *A* to *B* than it will from *B* to *A*, with the result that the liquid will rise in *B* and fall in *A*. The higher the concentration of the sugar solution, the higher will the liquid rise in *B*. Similarly, if two sugar solutions of different concentrations are separated by a membrane permeable only to water, water will move more rapidly toward the side of greater concentration of sugar and will set up a pressure on that side, which will raise the piston. In the figure we could keep the level of the liquids equal by applying pressure to the piston on side *B*. This pressure would have the effect of speeding up the molecules in side *B* so that, even though there are fewer water molecules per unit volume on this side of the membrane, their

increased speed would be such as to cause as many molecules of water to move from *B* to *A* as are moving from *A* to *B*. *The phenomenon, which results in a difference in rate of movement (or passage through the membrane) of solvent molecules from opposite sides of a selectively permeable membrane separating two solutions of different concentrations, is called osmosis.* The increased pressure resulting on the side of greater concentration is called **osmotic pressure**. The magnitude of osmotic pressure that can be developed by a given solution will depend upon the concentration of the solution as well as upon other factors.

It should be noted here that it is not the diffusion of the dissolved substance that is significant in osmosis but rather the movement of the water molecules. When solutes diffuse through a membrane, the phenomenon may be correctly called diffusion rather than osmosis. The term "osmosis" is thus restricted to conditions that result in osmotic pressure. Osmotic pressure will be set up only when the membrane is selectively permeable or when the membrane permits water to pass more freely than it permits solutes to pass. In the latter case, the osmotic pressure set up will always be only temporary. *The term "osmotic pressure" is commonly used as a physical constant of a solution.* Thus we say that a liter of a solution containing a molecular weight in grams of any substance that does not ionize (*i.e.*, a nonelectrolyte) has an osmotic pressure of 22.4 atmospheres, meaning that a maximum osmotic pressure of 22.4 atm. would be developed if this solution were separated from its pure solvent by a membrane permeable only to the solvent. *When the osmotic pressure of a solution is given, therefore, it always means the maximum osmotic pressure that this solution could develop when separated from its pure solvent by a membrane permeable only to the solvent.*

THE GENERAL WATER RELATIONS OF THE CELL

The fact that plant cells are always completely enclosed structures introduces several additional forces that must be considered if we are to understand the mechanism of absorption by a cell. Mature living plant cells usually consist of a cell wall, which is permeable and elastic, a peripheral layer of protoplasm, which is selectively permeable, and a large central vacuole containing a solution of organic and inorganic solutes (Fig. 51).

By virtue of the osmotic pressure of the cell sap, such a cell, when immersed in pure water or in a solution of lower concentration than that of the cell sap, is capable of absorbing water by osmosis and increasing in volume. As the cell enlarges, the wall stretches and, being elastic, tends to return to its original shape. That is, the wall resists extension and hence exerts

an inward pressure which opposes the entrance of water. This force is called **wall pressure**. Further expansion of the cell will cease when the wall pressure is great enough to cause water to be forced out of the cell as fast as it is taken in by osmosis. When a cell is stretched in this condition, it is obvious that the liquid within the cell is pressing out against the cell wall. This actual hydrostatic pressure of the cell content against the wall is called **turgor pressure**. Turgor pressure obviously tends to force water out of the cell. When equilibrium is established, *i.e.*, when the cell is neither increasing nor decreasing in volume, the turgor pressure just balances, *i.e.*, is equal to the wall pressure. It should be noted here that the turgor pressure is not the same as the osmotic pressure of the cell. The osmotic pressure is the maximum pressure which the cell could exert by virtue of its concentration of solutes if the cell were immersed in pure water. Turgor pressure can, under proper conditions, equal the osmotic pressure, but it can never exceed it. When a cell is not yet fully turgid, *i.e.*, when the turgor pressure has not yet reached its fullest expression, it is capable of absorbing water from the exterior. The net force sending water into the cell in this case is equal to the difference between the osmotic pressures of the cell sap and the external solution minus the actual pressure (turgor pressure) already existing within the cell. This net force is sometimes called the **net suction force** of the cell. If we represent it by S and represent turgor pressure by T , internal osmotic pressure by P_i , and external osmotic pressure by P_e , the relation between these forces is given by the equation $S = (P_i - P_e) - T$. The term "suction force" was apparently derived from a literal translation of the German word *Saugkraft*. A better term for this force would probably be simply "water-absorbing power." By some authors it is called "diffusion pressure deficit."

If a cell is immersed in a solution of greater concentration than that of the cell sap, obviously water will move out of the cell faster than it moves in and the cell will shrink in volume until the protoplasm actually shrinks inwardly, away from the cell wall. When this occurs, the cell is said to be **plasmolyzed**. It is clear that the potential osmotic pressure of a plasmolyzed cell is very high, while the turgor pressure is zero.

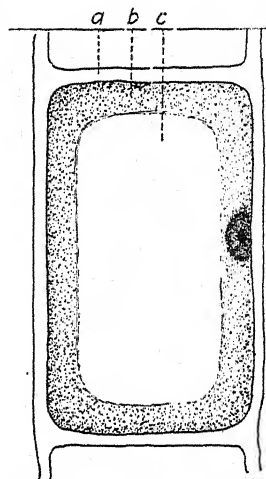


FIG. 51. Diagram of a mature living plant cell; a, cell wall; b, peripheral protoplasm; c, central vacuole containing a solution of organic and inorganic solutes, the cell sap. (Drawing by F. Brown.)

ABSORPTION OF WATER AND INORGANIC SALTS BY LOWER PLANTS

Having considered the principal forces involved in absorption in general, we are now in a position to take up the manner in which plants make use of these forces in obtaining water and inorganic salts from the external medium. It should be emphasized at the start that water moves independently of the movement of dissolved substances. Furthermore, each particular solute moves independently of all others.

In plants growing submersed in water, such as many of the algae, the problem of absorption of water and mineral salts is comparatively simple. Each cell of such a plant usually absorbs its water and minerals directly from the external medium. Water moves in by osmosis and inorganic salts diffuse in through the plant-cell membranes. The water relations are those already described for the cell.

ABSORPTION OF WATER BY VASCULAR PLANTS

In the higher vascular plants the problem of absorption is much more complex because these plants are accustomed to a land habitat. Whereas an animal can move about from place to place to satisfy its needs, the plant must remain fixed in one position and rely on materials being brought to it. While the higher plants, unlike animals, make all their own food, they must depend upon the environment for water, inorganic salts, carbon dioxide, and oxygen. In these plants the special problem of obtaining water and inorganic salts has been accomplished by the development of an extensive root system. This root system alone remains in contact with the supply of water and minerals.

Condition of Water in the Soil. Soil consists of weathered rock particles of various sizes together with more or less organic matter derived from the decay of plants and animals. Various microscopic living organisms, such as bacteria, protozoa, algae, and fungi, are also found in soil and play a prominent part in the relation of soil to higher plants. Depending upon the size of the predominating particles present, soils may be classified as gravelly, sandy, silty, or clayey. If equal amounts of all these various sizes of particles occur, the soil is said to be a loam. All soils contain many pores or air spaces in which oxygen, carbon dioxide, and other gases are found.

When water in the form of rain falls upon a soil, some of it runs off the surface, some sinks freely in response to gravity, the so-called **gravitational** or **free water**, while a considerable portion will adhere as a film to the soil particles. Of the last portion, the part which is free to move by capillarity from one soil particle to another, as evaporation occurs at the surface or as water is removed from adjacent regions of the soil, is called **capillary water**. Even after a soil has become air dry a certain

amount of water will still remain in the form of very fine films on the soil particles. This is called **hygroscopic moisture**. The amount of hygroscopic moisture and the freedom of movement of the capillary water will depend upon the size of the soil particles, the chemical nature of the particles, the amount and nature of the organic matter present, and other factors. In any case, when water is lost from a given region of the soil either by evaporation from the surface or by being absorbed by the roots of plants, the capillary water from adjacent regions tends to move toward that region because of ordinary capillary action. As this is a mass movement of water, it carries with it any substances in solution in the water. In other words, as the root absorbs water from the soil, some water may move toward the root from adjacent regions by capillarity, provided there is an abundance of water in the soil. Capillary movement of water, however, may be very slow and may be inadequate to supply the needs of a rapidly transpiring plant. If a soil dries out sufficiently, a condition may be reached when the soil particles themselves hold the water with sufficient force to prevent an adequate movement to the plant. Under such circumstances, unless water is added to the soil, the plant will wilt. Even though the plant wilts under such conditions, there is still a considerable amount of water left in the soil. The percentage of water left in the soil when plants permanently wilt in it under ordinary conditions is called the **wilting coefficient** of the soil. The wilting coefficient varies with different kinds of soil.

Water does not exist in a pure form in soil but is a solution containing various solutes, chiefly inorganic, commonly referred to as the **soil solution**. The osmotic pressure of the soil solution, while quite variable, averages around 0.2 to 1 atm. in humid regions. Naturally, as a soil dries out, the soil solution becomes more concentrated and its osmotic pressure increases accordingly.

Absorption of Water by Root Hairs. In the higher vascular plants water is absorbed chiefly through the root hairs or through the very young roots when root hairs are absent. The structure, position, and development of the root hairs have been mentioned on a previous page. There remains to be considered how they function in absorption.

The walls of the root hairs (Fig. 52) are not only thin but possess an external layer consisting largely of a hydrophilic colloid, calcium pectate, or other pectic material, which readily absorbs water by imbibition from the soil solution. This imbibed water furnishes a channel for the osmotic movement of water as well as for the movement of inorganic salts, since the wall itself is permeable. Just inside the wall of the root hair is a thin layer of protoplasm, colloidal in nature, which surrounds usually a single large central vacuole. While this protoplasmic membrane is permeable to most

mineral salts, it is not permeable to many of the organic solutes inside the cell and hence behaves as a selectively permeable membrane. The large central vacuole contains cell sap which is a complex solution of inorganic and organic solutes among which may be mentioned sugar. The total concentration of all solutes in this cell sap is such as to give it an osmotic pressure of at least 4 to 10 atm. Since the osmotic pressure of the soil solution in humid regions is seldom over 1 atm. and since the protoplasmic

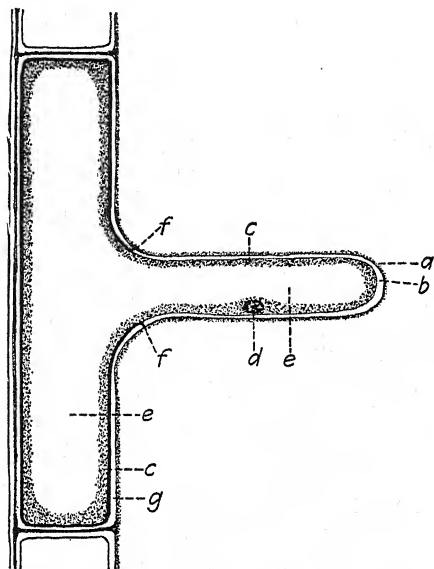


FIG. 52. Diagrammatic lengthwise section through a root epidermal cell showing origin and structure of a root hair; a, outer wall layer of pectic material, continuous with that of the wall of the epidermal cell and the middle lamella of adjoining cells; b, inner wall layer, considered callose by some investigators and cellulose by others; c, peripheral cytoplasm; d, nucleus; e, central vacuole containing cell sap; f, point at which root hair burst through the cellulose layer of the epidermal cell from which it originated; g, cellulose layer. (Drawn by F. Brown.)

membrane is selectively permeable with respect to many of the solutes inside the cell, it is obvious that there will be relatively more water molecules moving into the root hair at any given time than are moving out or, in other words, water will be taken up by osmosis. The root hairs grow out into the pore space of the soil and, like the soil particles, become surrounded by films of water. As these films are removed by absorption by the root hairs, the films of adjacent soil particles are drawn on. These in turn draw on films of the particles adjacent to them, and thus water may move from considerable distances to the root hairs. During active transpiration, or loss of water vapor from the plant, there is set up in the xylem a negative pressure or tension which probably promotes the entrance of water into the root hairs. It should be noted that water is not simply "sucked in"

by root hairs but moves in of its own accord by virtue of the kinetic energy of its molecules.

Transfer of Water to the Xylem. It will be recalled that root hairs are merely outgrowths or parts of epidermal cells. The epidermal cells are adjacent to the cortical cells and these extend to the endodermis. Inside the endodermis is the single layer of cells called the pericycle. At the protoxylem points of the root the pericycle lies next to the xylem. This

offers a direct channel for the passage of water and inorganic salts to the xylem at these points without the necessity of their passing through the phloem. As the water is absorbed by the root hairs, the root-hair cells tend to become more and more turgid. As the turgor pressure rises in them, water passes from the root-hair cell to the first cortical cell in contact with it. This cell in turn passes the water on to the next cortical cell and so on until it reaches the xylem. There is probably a gradient of suction force extending from the root hair to the xylem. As already mentioned in the preceding paragraph, the tension set up in the xylem by transpiration probably also promotes the transfer of water from root hairs to xylem. Through the xylem the water is carried to all parts of the plant.

ABSORPTION OF INORGANIC SALTS BY VASCULAR PLANTS

Inorganic Salts Required by Plants. From the soil, vascular plants obtain, besides water, inorganic salts that are essential in the general metabolism of the plant. Knowledge of what minerals are required by green plants has been obtained by growing plants in solutions of known composition. Cultures in such solutions are commonly called **water cultures**, or **solution cultures**. The growing of plants in solution cultures is sometimes called **hydroponics**. It was very early discovered that, for the plant to be able to grow well, such solutions had to contain salts of phosphorus, potassium, nitrogen, sulfur, calcium, iron, and magnesium. These elements, together with carbon, hydrogen, and oxygen, were looked upon as the 10 essential elements for plant growth, the carbon being obtained from carbon dioxide of the atmosphere, the hydrogen from water, and the oxygen partly as a gas from the atmosphere. Later work has demonstrated that there are probably many more than 10 essential elements. Thus there is evidence that plants must also have salts containing such elements as sodium, silicon, chlorine, manganese, and very minute quantities of boron, zinc, copper, aluminum, molybdenum, and iodine. Elements that are used in very minute quantities by plants are referred to as "microelements" or "trace elements." Some of the microelements, notably copper and zinc, probably function as prosthetic groups for enzymes (see page 307).

Condition of Inorganic Salts in the Soil. The inorganic salts that are absorbed by plants are found dissolved in the soil solution. Most of them probably exist as ions, such as NO_3^- , SO_4^{--} , PO_4^{---} , Cl^- , NH_4^+ , K^+ , Ca^{++} , Mg^{++} , Fe^{+++} , and others. Some of these ions are held on the surfaces of the soil particles by adsorption, a surface force common to such small particles. The presence of various colloids in the soil helps to increase the amount of adsorption and tends to prevent the leaching

out of mineral salts that are needed by plants. Leaching out of inorganic salts is rather pronounced in a loose sandy soil containing little organic matter. Some ions, particularly SO_4^{--} , NO_3^- , and Cl^- , are held so weakly that they leach out readily and are lost in the drainage waters. Others, like PO_4^{--} , K^+ , and NH_4^+ , are held more firmly.

Some of these salts exist in forms that are not available to the plant. The chemical and physical forces operating in the soil, enhanced by activities of soil organisms, are important factors in rendering such salts available. This is of particular significance with regard to nitrogen. Nitrogen may exist in the soil in the form of gaseous nitrogen, ammonia, nitrates, nitrites, or complex organic forms such as occur in the soil humus. The nitrate form is the one most available to ordinary plants. While many plants probably absorb ammonium salts, gaseous nitrogen and organic nitrogen compounds are usually unavailable as such.

Nitrification. Fortunately there exist in soils several groups of bacteria that are capable of converting the unavailable organic nitrogen into available nitrates. The process by which this is brought about takes place in several steps involving different kinds of bacteria and is called **nitrification**. In the first step in the process, the proteins of the soil organic matter are broken down to amino acids. This occurs during ordinary decay of organic matter and is brought about chiefly by bacteria and fungi. In the next step, by a process called **ammonification**, a group of bacteria known as **ammonifying bacteria** together with certain fungi convert the amino nitrogen to ammonia. The ammonia thus formed would escape from the soil in gaseous form were it not for the fact that other chemicals present in the soil react with it to form ammonium salts. Among these may be mentioned ordinary carbon dioxide and water, with which ammonia forms ammonium carbonate. In the third step of the process, the ammonia of the ammonium salts is oxidized to nitrite by bacteria known as the *Nitrosomonas* group. Finally the *Nitrobacter* or nitrate group of bacteria oxidizes the nitrite to nitrate. Thus nitrification finally results in the conversion of unavailable organic nitrogen to available nitrates. It should be observed here that nitrification does not increase the amount of nitrogen in the soil. It may actually result in a loss of nitrogen by leaching.

Nitrogen Fixation. Ordinary plants are unable to utilize atmospheric nitrogen. There exist in the soil, however, two types of bacteria that are able to assimilate the atmospheric nitrogen in soil air by converting it into proteins. These bacteria are known as **nitrogen-fixing bacteria**, and the process by which they assimilate free nitrogen is called **nitrogen fixation**. One type of these bacteria lives independently in the soil. Two prominent genera of this group are *Azotobacter* and *Clostridium*. The other type,

consisting of species of *Rhizobium*, lives in enlargements called tubercles, or nodules, on the roots of leguminous plants such as peas, beans, and clover. Both of these groups tend to increase the amount of nitrogen in the soil. In the free-living forms, the proteins formed from the atmospheric nitrogen are left in the soil when the organisms die and by nitrification are made available to higher plants.

The nodule-forming group, sometimes called symbiotic nitrogen fixers, enter the roots of legumes chiefly through root hairs and gradually work their way inward by means of an "infection thread" to the cortical cells. Here they cause abnormal growth which results in the well-known nodules, or tubercles. The bacteria feed on the carbohydrates and other food of the legume and undergo a change in form, considered a type of degeneration resulting in V- and Y-shaped organisms. In this condition they utilize atmospheric nitrogen to synthesize proteins. Some of this nitrogen becomes available to the leguminous plant in which the bacteria are growing. When the plants are harvested, the roots containing the bacteria are left in the soil and when they decay, the organic nitrogen made by the bacteria becomes available nitrate through the process of nitrification. Each type of legume seems to require a particular strain of bacteria in its roots. If this strain is not present in the soil, it can be added artificially. Usually this is done by inoculating the seeds before they are sown.

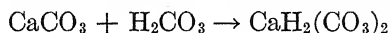
From what has been brought out it is clear that a leguminous crop in a rotation possesses an advantage besides that of the value of the crop itself, since it increases the amount of nitrogen in the soil. This is one of the principal reasons why soybeans or sweet clover are used in a potato rotation or clover and alfalfa in an ordinary field-crop rotation.

Denitrification. In addition to nitrifying and nitrogen-fixing organisms of the soil there are others that bring about a reverse process which results in the breaking up of nitrogenous substances with the liberation of free nitrogen gas. These are called **denitrifying** organisms. Fortunately these organisms are chiefly anaerobes; *i.e.*, they live in the absence of free oxygen and do not thrive when good aeration is maintained. Consequently, so long as a soil is kept in a good state of cultivation the denitrifiers are suppressed and the nitrifying and nitrogen-fixing organisms are favored, leaving a balance of available nitrogen for higher plants.

Effect of Roots on the Soil. Roots, themselves, growing in the soil have important effects on the chemical and physical nature of a soil which directly or indirectly affect absorption of inorganic salts by the plant. Thus it has already been stated that the decay of roots furnishes available nitrogen and other substances for later crops. By this means considerable amounts of organic matter are added to the soil each year. This organic matter influences both the physical and chemical properties of the soil in

addition to furnishing available solutes. Sometimes, however, complex organic compounds are formed from either living or decaying roots which prove to be toxic to later plants. These substances may be toxic only to the kind of plant which produced them. In such cases crop rotation overcomes the injurious effects of the toxic substances.

All living roots, in the process of respiration, give off fairly large quantities of carbon dioxide, CO_2 . This carbon dioxide, uniting with water, forms carbonic acid, H_2CO_3 , which acts as a weak solvent for some substances that would not readily dissolve in water alone. Thus it can be shown that, after roots have been grown on a polished marble plate, the plate will be etched in all places where the roots came in contact with it. This etching is caused by the conversion of the relatively insoluble calcium carbonate, CaCO_3 , or marble, to the more soluble bicarbonate, $\text{CaH}_2(\text{CO}_3)_2$, according to the following equation:



This reaction takes place regularly in all limestone soils. The carbonate ion may also be exchanged by the root for NO_3^- or other ions needed by the plant.

The lower organisms in a soil also give off carbon dioxide in respiration. It is possible for the carbon dioxide content of the soil air to become great enough to be injurious to plants. This is caused partly through the relative decrease in oxygen content of soil air under these conditions. In a well-aerated soil, the excess carbon dioxide escapes to the atmosphere where it may be absorbed by the leaves and utilized in photosynthesis.

Factors Affecting the Absorption of Inorganic Salts by Roots. The processes involved in the absorption of inorganic salts by the root hairs are exceedingly complex and not yet well understood. They probably involve simple diffusion. The mere fact that a mineral is absorbed indicates that the protoplasmic membrane of the root hair is permeable to it. This being true, it is obviously erroneous to speak of the entrance of minerals as taking place by osmosis. Minerals are not simply swept in with the water but diffuse in independently of the movement of water. In fact, it is possible for a mineral to be moving out of the root hair while water is moving in.

It has already been stated that part of the minerals of the soil exist dissolved in the soil solution. Only dissolved minerals are free to diffuse into the root hair. Yet not all dissolved minerals are equally able to enter. If the root-hair membrane is not permeable to them they will not be able to enter at all, even though they are in solution. Furthermore, the fact that the membrane is more permeable to some than it is to others will affect their rate of entrance. In general, any mineral to which the root-hair membrane is permeable may enter, even though it may be injurious to the plant. Thus, if a sufficiently strong solution of copper sulfate, zinc sulfate, or other soluble toxic substance to which root-hair membranes are permeable is brought into contact with a root, it will be absorbed by the root hairs even though it kills the plant. The plant, in other words, has no power to select only such substances as are useful to

it. Sometimes a plant will absorb a relatively useless ion more readily than a useful one. Thus sodium is absorbed by barley plants from some solutions much more readily than calcium is, and chlorine is more readily taken in than sulfate, even though sodium and chlorine may be less useful to the plant than calcium and sulfate. For this reason we may find substances in plants that probably are of no particular use to them but which existed in the soil solution and could not be excluded because the root-hair membrane was permeable to them.

One of the laws of diffusion states that a dissolved substance will always move more rapidly from a region of high concentration of that substance to one of lower concentration. Consequently, in order for a mineral to be absorbed it must exist in higher concentration in the soil solution than in the cell sap of the root hair; otherwise the root hair would lose this mineral to the soil solution. It should be remembered here that each solute moves independently of the others and according to the relative concentration of that particular solute in the soil solution and in the root hair. For instance, if sodium nitrate is to be absorbed by the root hair, there must be a higher concentration of sodium nitrate in the soil solution than in the root hair, regardless of the concentrations of all other minerals.

If all the minerals that are absorbed by the root hair were to remain in the root-hair cell, a concentration would soon be reached which would cause these minerals to move out of the root hair as fast as they are moving in and further net absorption would cease. This condition, however, probably does not occur because the minerals are free to diffuse inward to the adjacent cortical cells of the root. As soon as the concentration of a particular mineral becomes greater in the root-hair cell than it is in the adjacent cortical cell, this mineral will diffuse into the adjacent cortical cell. Similarly this latter cell will pass the mineral on to the cell adjacent to it and thus the minerals diffuse from cell to cell until they reach the xylem. There is thus established a decreasing concentration gradient of each mineral from the root hair to the xylem which permits a continuous absorption of mineral salts from the soil solution.

In many of the lower plants growing in water, the absorbed minerals do remain in the cells in which they are absorbed. We should therefore expect to find that a concentration of a particular mineral would soon be reached which would equal the concentration of that mineral in the medium from which the mineral was obtained and that this would prohibit the entrance of any more of this mineral. Apparently, however, there are cases in which this is not true. For example, the common fresh-water alga *Nitella* lives in a medium in which the chlorine content varies between 20 and 30 parts per million; yet the cell sap of the alga may have a concentration of chlorine of 3,500 parts per million. Moreover, under suitable conditions all the chlorine in the medium may be taken up by the alga, yet none will pass out of the cell unless it is injured. Here we have an apparent contradiction of one of the laws of diffusion inasmuch as the chlorine seems to be taken up against a concentration gradient. A satisfactory explanation of this situation is difficult to find although it is possible that as soon as the chlorine enters the cell it is changed to a form to which the cell membrane is not permeable. Whether this situation may occur also in root hairs is not definitely known.

Some of the inorganic salts occurring in the soil solution are in an ionized condition. Thus sodium nitrate, NaNO_3 , may ionize as Na^+ and NO_3^- ions. The two ions of a salt are not necessarily absorbed in equal proportions. Any large absorption of one ion in excess of another of opposite charge in equilibrium with it depends upon what in effect amounts to an exchange of ions between the soil solution and the root hair. If, for example, an excess of K^+ ions is absorbed from potassium sulfate, other cations like Na^+ , Ca^{++} , or Mg^{++} may be displaced from the root hair. Similarly, NO_3^- ions

or Cl^- ions may be absorbed and HCO_3^- ions from the plant exchanged for them. The production of carbon dioxide by roots may therefore play an important role in mineral absorption by the plant. It is also possible for a particular ion to retard or accelerate the absorption of another ion. Thus K^+ is absorbed by barley plants much more readily from the chloride (KCl) than from the sulfate (K_2SO_4). A relatively high concentration of Na^+ may depress the absorption of K^+ or Ca^{++} , and the presence of Ca^{++} may influence the entrance of Mg^{++} , K^+ , or Na^+ . This influence of one ion upon another is called **antagonism**. The acidity or alkalinity of the soil solution and many other factors probably also affect the entrance of inorganic solutes.

In general, the relation between the root hair and the soil solution is a very complex one and the mechanism of absorption by higher plants difficult to understand. Recent work has demonstrated that the absorption of inorganic substances by the plant is not merely a physical process but is probably a complex physiological process in which respiration plays a dominant role.

Fertilizers. The composition of the soil solution varies greatly in different places and in the same locality at different times and under different conditions. Inorganic salts of such elements as iron, magnesium, sodium, chlorine, silicon, sulfur, manganese, and aluminum exist in available form in most soils. It is not at all uncommon, however, to find soils deficient in one or another of such salts as contain an available supply of potassium, phosphorus, and nitrogen. This is partly caused by the fact that plants probably absorb greater quantities of these minerals and partly because some of these salts are easily leached out of the soil. Sulfur may also be deficient in some soils, and in particular localities iron, magnesium, or manganese may be in such forms as to be unavailable to the plant. Minerals added to the soil to correct such deficiencies are called fertilizers. While fertilizers are added to soil for a variety of reasons, undoubtedly one of the principal functions is to furnish the plant with available inorganic salts. Fertilizers may be added in the form of farm manure, which contains most of the elements likely to be deficient in a soil, green manure, a green crop, preferably a legume, ploughed under, and commercial fertilizers which consist of salts of potassium, phosphorus, or nitrogen. A commercial fertilizer containing salts of all three of these elements is called a complete fertilizer. Nitrogen is added in such forms as sodium nitrate, ammonium sulfate, and many organic forms. Potassium is found in fertilizers in the form of potassium chloride or potassium sulfate and phosphorus chiefly as phosphates. Sulfur is usually added in the form of gypsum. Lime is commonly added to soil to correct acidity and to improve the structure of the soil but the calcium it contains is also very important in the life of the plant.

Utilization of Inorganic Salts by the Plant. Many of the inorganic salts the plant gets from the soil are used as raw materials out of which foods and other important plant constituents are made. The exact functions of each of the elements absorbed are not well known. Most of our knowledge of this matter has been obtained by the examination of plants grown in the absence of one or another of the minerals. Practically nothing is known as to the manner in which a plant utilizes such ions as sodium, chlorine, boron, zinc, iodine, and others taken up in very minute quantities. It is customary to speak of the functions of the essential elements. It should be remembered that, when this is done, it is the compounds containing these elements that is meant. None of the elements is absorbed as such.

Manganese is thought to be necessary for the proper function of respiratory enzymes in the plant. Recently it was found that a chlorotic condition of spinach, *i.e.*, a yellowing of the plant caused by the failure of chlorophyll to develop, could be overcome by adding manganese salts to the soil.

Iron and *magnesium* are necessary for chlorophyll formation. Magnesium is a constituent of the chlorophyll molecule but iron is not. Just why iron is necessary for chlorophyll formation is not exactly known. Some soils, while containing an abundance of iron, have it in a form unavailable to the plant. Plants grown in such soils cannot develop chlorophyll and therefore do not thrive. The difficulty is usually overcome by spraying such plants with iron sulfate. Iron may also function in respiration. High concentrations of magnesium are toxic to plants.

Phosphorus is a constituent of many organic compounds of the plant, such as phosphoproteins and phospholipides. Since the nuclei of cells contain phosphorus, lack of this element probably interferes with normal cell division and therefore checks growth. The combining of phosphates with sugars and other compounds plays a dominant role in the transformations of carbohydrates in the general metabolism of the plant. Phosphorus seems to increase root development and in many plants hastens maturity and ripening, particularly of grains.

Potassium seems to be necessary for the proper carbohydrate metabolism of the plant. Whether it directly affects the synthesis of carbohydrates or is chiefly of importance in facilitating the digestion and translocation of carbohydrates is not well known. At any rate, when potassium is deficient, storage organs such as roots, tubers, and seeds become small and shriveled. Potatoes, being chiefly a carbohydrate crop, give increased yields with ample potash fertilization. It has been shown that in potash-starved plants the sieve tubes of the phloem, through which carbohydrates are carried to the different parts of the plant, degenerate to some extent. When plants have an ample supply of potassium, they have been reported to be more resistant to disease and insect injury.

Nitrogen is used chiefly in the building of proteins. Since all proteins contain nitrogen and since proteins are present in every living cell, the importance of an available supply of nitrogen to the plant is evident. It is absolutely essential to growth, affecting particularly the growth of the aboveground parts of plants. Nitrogen is also a constituent of chlorophyll. A deficiency of nitrogen soon manifests itself in the color of foliage, which becomes yellowish. Excess of nitrogen may cause excessive vegetative growth, which results sometimes in weak stems and tender, juicy foliage which is more susceptible to insect and fungus injury. In such crops as lettuce and cabbage, increased growth of this kind, if not carried to excess, may be an advantage, but in crops grown for seed, fruit, or storage organs, such as grain crops, tomatoes, and potatoes, it is a decided disadvantage since vegetative growth is enhanced and fruit and seed development and food storage are suppressed. Grain crops like wheat, oats, and barley have also a greater tendency to lodge when supplied with excessive nitrogen.

Calcium, usually added to soil in the form of lime, plays a very prominent part in absorption of minerals generally from the soil. In the first place, it neutralizes acids which otherwise would prevent proper absorption of minerals. It also has an anti-toxic effect on many poisonous substances in the soil, thereby preventing them from injuring the plant. Through its influence on the soil colloids it tends to loosen the soil in such a way as to provide better aeration, better drainage, and a more favorable temperature. In this way it facilitates root growth. In the actual process of absorption it is very important not only because it influences the entrance of other minerals but, through the formation of calcium soaps and calcium proteinates, it has much to do with maintaining the semipermeability of plant-cell membranes. In the absence of calcium the plant not only is unable to take in the needed minerals but allows many of the substances present in the root hair to escape. It has already been mentioned that the root-hair cells contain calcium pectate, a hydrophilic colloid which enables

them to imbibe water. This substance also forms the cementing material for holding cells together throughout the plant and is usually the first substance laid down in the formation of new cell walls. Consequently a supply of calcium is essential to good growth. In its absence, the meristematic regions of the plant at the growing tips die. The general vigor of the plant is greatly influenced by calcium. In the cells of the plant it often unites with acids which result from ordinary metabolism, thereby neutralizing them and preventing any harmful action from them. Thus calcium oxalate crystals are found quite commonly in plants, having been formed by the union of calcium and oxalic acid. In these and in other ways calcium plays a dominant role in the life of the plant.

Sulfur is a constituent of at least three of the amino acids that occur in proteins. Since almost all the proteins naturally occurring in plants contain these amino acids, it is clear that sulfur is necessary for protein synthesis. The mustard oils, occurring particularly in the mustard family (Cruciferae), also contain sulfur. Recently a substance has been discovered in cells that has been called **glutathione**. Glutathione is an autooxidizable substance which can take up oxygen from the atmosphere which may be yielded to other compounds in the cell and result in their oxidation. In this way glutathione may play a prominent part in respiration. These properties of glutathione rest upon the sulfur groups it contains. Sulfur is probably important to plants in other ways also. While most soils contain enough sulfur to supply the ordinary needs of plants, there are some localities in which sulfur is deficient in the soil. In parts of Washington and Oregon, greatly increased yields of alfalfa and other crops have been obtained by adding gypsum, CaSO_4 , to the soil. These increased yields are attributed largely to the sulfur which gypsum contains.

In conclusion, it should be emphasized that if the plant is to do its best it must be supplied with a proper balance of all the essential inorganic salts. If one of the inorganic salts is deficient, its lack will soon be manifested in the growth of the plant regardless of how much of all the other salts may be available.

CHAPTER 8

STEMS

GENERAL FEATURES

Distinguishing Features of Stems. The stem is that organ of the plant which typically serves as a mechanical support for the leaves, flowers, and fruits and furnishes a path of conduction between these organs and the roots. While most stems are erect aerial structures, some remain underground, others creep along the surface of the ground, and still others are so short and inconspicuous that the plants bearing them are said to be stemless. Morphologically, stems have certain external features by means of which they can be distinguished from other plant parts and particularly from roots, with which they are most likely to be confused, especially when underground. True stems arise from buds, they have nodes and internodes, they bear leaves and buds and sometimes roots at the nodes, and they have characteristic markings, such as leaf scars, bud-scale scars, and lenticels (Fig. 56). These external features are considered in greater detail in succeeding paragraphs. Internally, stems are characterized by having a highly developed vascular system. Stem-like structures of lower plants lack the external markings and other features of true stems and have no vascular system.

Origin and Growth of Stems. Stems, like leaves, develop from buds. In plants grown from seed it is the rudimentary bud of the young plant in the seed that forms the first vegetative shoot. This first bud is called the plumule and may consist merely of a mass of meristematic tissue or may already be differentiated into stem and leaves. In the seedling, as well as in older plants, the branches are developed chiefly from axillary buds. Growth in length of stems results from the activity of meristematic regions of terminal or lateral buds and consists not only of an increase in the number of cells but also in enlargement of cells already found in the bud. Consequently the stem tip may be divided into zones comparable with those of the root. There is, however, no structure like a rootcap over the meristematic region of the stem. As a rule, the leaves of several nodes of the stem are folded over the stem tip in such a way as to protect this region even in actively expanding buds (Fig. 60). Whereas the region of elongation of the root averages around 2 to 10 mm. in length, that of the growing stem is often 2 to 10 cm. long and involves

several nodes and internodes (Fig. 53, A). Below this growing region at the tip, the tissues become fully differentiated and then cease to elongate, although in dicotyledonous plants and gymnosperms, growth in diameter of the stem continues. In monocotyledonous plants, elongation occurs at the bases of the internodes near the tip as well as at the tip of the stem (Fig. 53, B). In many trees and shrubs, the total growth in length of the stems during any one year occurs during a very short period in the spring.

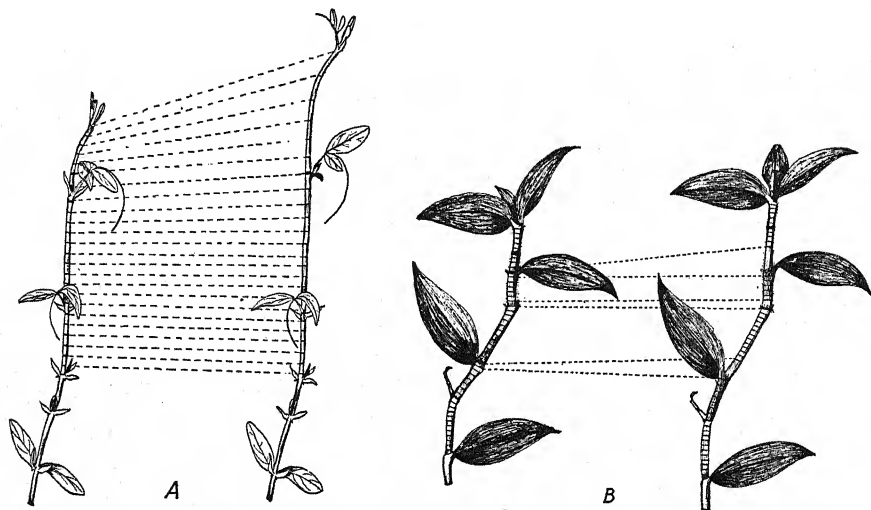


FIG. 53. A, region of elongation of the stem of a dicotyledonous plant, sweet pea (*Lathyrus odoratus*). The stem tip at the left is shown as originally marked into 2-mm. zones. At the right the same stem is shown as it appeared 2 days later. Note that growth in length is restricted to the upper nodes and internodes, in this case involving about 24 mm. of the stem tip; B, region of elongation in the stem of a monocotyledonous plant (*Tradescantia zebrina*). The plant at the left is shown marked into 2-mm. zones, and at the right is shown its appearance after 3 days. Note that the principal elongation, indicated by the dotted lines, occurred at the base of each of the internodes near the tip. The growth at the apex is concealed by the leaves. Elongation at the base of the internodes results from the activity of intercalary meristems. (Drawings by F. Brown.)

During the remainder of the growing season, new buds are differentiated at the stem tips and in the leaf axils.

Buds. Buds, as previously explained, are undeveloped shoots, often in a dormant condition. Sometimes they are merely undifferentiated masses of meristematic cells. In other cases, they are more elaborate structures, consisting of several nodes and short, unexpanded internodes, the whole enclosed by the closely packed, partly differentiated leaves. In perennial plants, the buds are dormant during the unfavorable growing conditions of late autumn and winter. At such times the more prominent buds are protected by a series of overlapping scales which are usually

highly modified leaves. **Bud scales** (Fig. 56, *B*) are often covered with hairs or wax, which increase their efficiency as protective organs. When buds are thus protected by scales, they are called **covered** or **protected buds** (Figs. 54, 55); those without scales are called **naked buds**. Herbaceous plants have naked buds. Covered buds are usually larger and more conspicuous than naked buds. Many buds are almost microscopic in

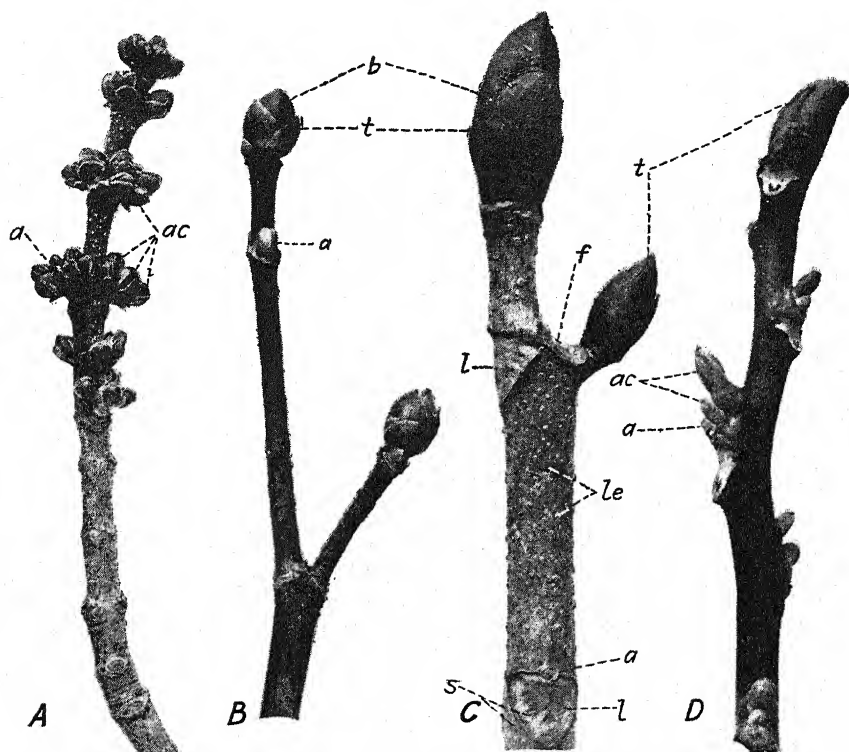


FIG. 54. Buds. *A*, silver maple; *B*, Norway maple; *C*, horse chestnut; *D*, butternut; *a*, axillary buds; *b*, bud scales; *ac*, accessory or supernumerary buds; *t*, terminal buds; all of these buds are covered or protected buds; *f*, fruit scar; *l*, leaf scar; *s*, vascular-bundle scars; *le*, lenticels.

size while others are very large. A head of cabbage, for example, is an unusually large bud.

The majority of the buds of a plant remain undeveloped for indefinite periods of time and for this reason are known as **dormant buds** in contrast to **active** or **developing buds**. They may never develop except under unusual conditions. If, for example, the end of a twig is broken off, buds which ordinarily would not have developed may produce a new growth of stem and leaves.

Some buds give rise only to vegetative shoots consisting of stems and leaves. Such buds are usually called **leaf buds**. Others may develop into flowers only. These are called **flower buds** or, since flowers develop into fruits, **fruit buds**. Still others give rise to both vegetative shoots and flowers and are called **mixed buds**. The so-called "fruit buds" of the apple are in reality mixed buds. Most axillary buds are leaf buds, while buds occurring at the tips of stems are often mixed buds, as in many of the terminal buds of the horse chestnut. Peaches and some maples produce separate flower buds.



FIG. 55. Opening buds of hickory showing bud scales folding back and leaves emerging.

According to their position on the stem, buds may be classified as **terminal**, **axillary**, **accessory**, and **adventitious**. In a strict sense, all buds of the stem except the terminal buds might be called lateral buds, but this term is most commonly used as a synonym for axillary buds.

Terminal buds, *i.e.*, buds occurring at the tips of branches, are found on most plants and are particularly conspicuous on many trees and shrubs (Figs. 54, 55). They are often the largest buds on the plant and usually give rise to the principal growth in length of plants or branches bearing them.

Axillary, or **lateral**, buds develop in the axils of leaves (Figs. 14, 56).

Their position on the stem is determined, therefore, by the phyllotaxy of the plant. Axillary buds are often inconspicuous because of their small size. The majority remain dormant, but the removal or death of a terminal bud often brings them into activity. Since the axillary buds that do develop usually give rise to vegetative shoots, the type of branching of a plant is closely related to the position of these buds on the stem and hence to the phyllotaxy of the plant. Thus, since maples have opposite leaves with a bud in the axil of each leaf, the branches are also likely to be opposite.

Some species of plants regularly produce above or beside the axillary buds additional buds called **accessory** or, sometimes, **supernumerary** buds. In the silver maple and in the peach, for example, accessory buds are produced on both sides of the axillary bud (Fig. 54, A). These accessory buds are the flower buds. In the butternut (Fig. 54, D) and in the walnut, accessory buds occur above the axillary bud.

Adventitious buds arise irregularly on the plant not only on the stem but also on the root and, in some species, on the leaf. When branches of willow are cut back, many of these buds arise near the cut surface; when cuttings of sweet-potato roots are planted, adventitious buds give rise to the shoots which develop into the new plants. *Bryophyllum* leaves placed on moist soil also develop shoots from adventitious buds in the leaf notches (Fig. 33). Adventitious buds thus serve to propagate plants vegetatively. They also give rise to the common water sprouts of apple trees and other species.

Nodes and Internodes. **Nodes**, as already mentioned in the chapter on leaves, are the places on the stem where the leaves arise. Axillary buds also occur at the nodes. The space between two succeeding nodes is called an **internode** (Figs. 14, 56). In most dicotyledonous plants there is no very great difference in appearance between nodes and internodes even in mature stems. In the monocotyledons, however, such as corn, the nodes, often called "joints," are swollen somewhat and stand out in contrast to the thinner internodes. The entire internode of the grasses is often encircled by the sheathing leaf base, so that the leaf appears to be borne at the next upper node (Fig. 17, III). The number of leaves at the node is specific for each kind of plant. The nodes of plants with opposite or whorled phyllotaxy usually stand out more prominently than do those of plants with spiral phyllotaxy. The internal anatomy of a node is often different from that of the internode because of the connection of the vascular system of the leaf with that of the stem.

Scars and Lenticels. **Leaf scars** are the marks left on the stems of deciduous plants where fallen leaves were attached (Fig. 56). They mark the place where the abscission layer was formed at the base of the petiole. These scars, if examined carefully, will show **bundle scars** (Figs.

54, C, s; 56, B) left by the broken ends of the vascular bundles which formerly passed out of the stem into the leaf petiole. There are often as many of these bundle scars as there are main veins in the leaf. The

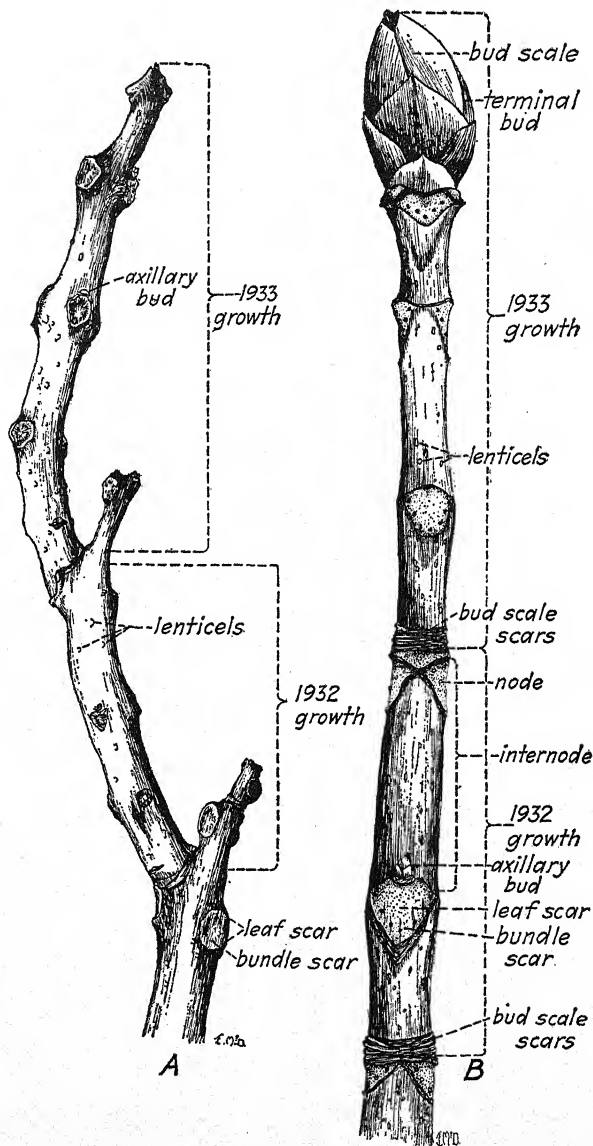


FIG. 56. A, twig of catalpa showing sympodial growth; B, twig of horse chestnut showing monopodial growth. Both twigs show characteristic stem markings. (Drawings by Elsie M. McDougale.)

shape of the leaf scar is specific for a given species of plant and may be used to some extent in identifying trees in winter.

Bud-scale scars occur in compact groups on the stem and mark the points of former attachment of the bud scales (Fig. 56, *B*). The individual scars are very small and narrow but, being closely grouped, together they form a rather conspicuous ring around the stem. The majority of them are left by terminal buds and, since new terminal buds are formed each year, the age and yearly growth in length of the stem can be determined by observing the number of these rings and the distance between them.

Flower and fruit scars (Fig. 54, *C, f*) mark the points of former attachment of flowers and fruits. They are sometimes quite conspicuous, as in the horse chestnut and in some fruit trees.

Lenticels appear on woody stems as small openings or pores, often slightly raised or ridged (Figs. 54, *C*; 56). They function in the exchange of gases between the interior of the stem and the surrounding atmosphere. The size and shape of the lenticels are often characteristic for a given species. They are particularly conspicuous on young stems. On the bark of cherry and birch trees and on elderberry stems, they appear as prominent transverse markings. Lenticels are multicellular structures (Fig. 76) often arising on the stem in positions previously occupied by stomata, which they replace after the epidermis ceases to function.

Size and Form of Stems. Stems exhibit wide variations in size, form, and structure. In length they vary from less than an inch to several hundred feet, the latter dimensions being attained by the giant redwoods of the Pacific Coast. In thickness they vary from almost hair-like structures to trunks of trees 50 ft. and more in diameter. Some stems are tender, fleshy, or watery, while others are hard and woody.

The classification of plants into **herbs**, **shrubs**, and **trees** (Fig. 57) depends upon the size and woodiness of stems. **Herbs** are plants with no persistent woody stem aboveground. Many are low-growing plants with succulent or fleshy stems. **Shrubs** and **trees** are perennials with woody stems, but shrubs are usually smaller than trees and consist of several main stems, while trees usually consist of a single main trunk or axis.

The large and conspicuous stems of trees assume various forms. The **columnar stem** is cylindrical, unbranched, and usually bears at its summit one set of leaves. The palms, bamboo, and numerous other monocotyledons have this type of stem (Fig. 58). Branching stems are of two types, **excurrent** and **deliquescent**. The **excurrent** type characteristically consists of one principal vertical stem, called the trunk, which tapers from base to summit. From it smaller horizontal branches radiate outward. Typically the lowest branches are the longest and oldest and the uppermost ones the

shortest and youngest, giving the whole plant a conical form (Fig. 59, *B*). Such evergreen trees as the spruce and the fir have the typical excurrent type of stem. The *deliquescent* type consists of a vertical main stem or trunk which rises for some distance above the ground and then divides into several branches which in turn branch again and again, making the trunk seem to melt away or deliquesce (Fig. 59, *A*). This is typical of the stems of many deciduous trees, as, for example, the oak, the maple,

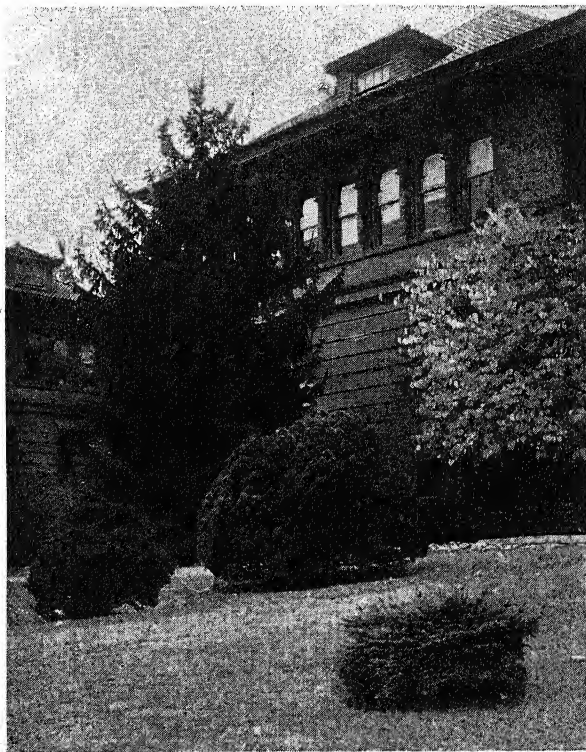


FIG. 57. View on the campus of the Pennsylvania State College, showing trees, shrubs, and herbs (herbs represented by the grass).

and the elm. There are many modifications of these principal types of stems. Mention should be made of the fact that when a tree is growing in the open its branching is likely to assume a different form from that found when trees are closely crowded together. In forests, the lower branches, particularly, are often crowded or cut off from sufficient light and hence do not develop normally. Consequently the main trunk grows to a greater height. The best development of the *deliquescent* habit is usually seen in trees growing in the open.

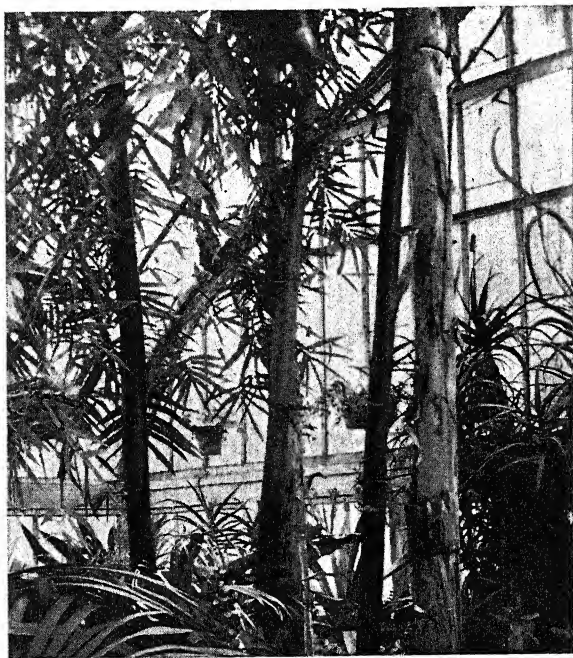


FIG. 58. Columnar stems illustrated by three stems of bamboo.

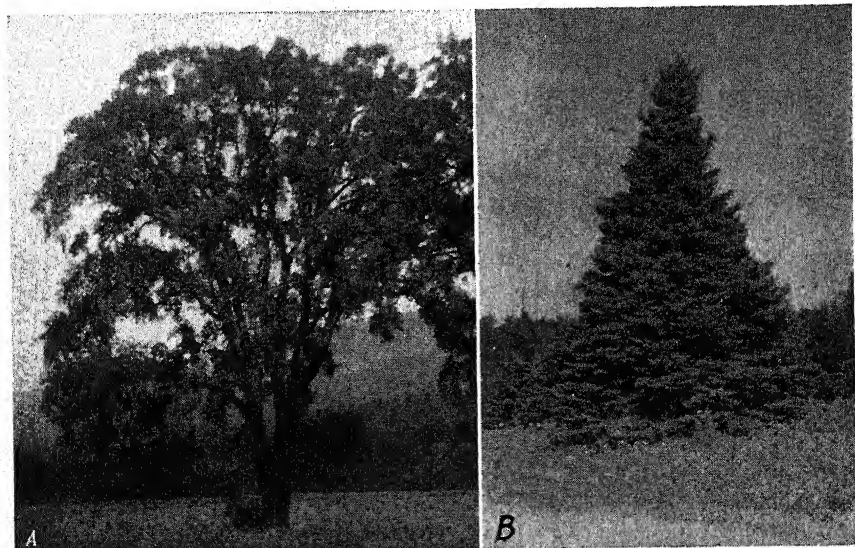


FIG. 59. A, deliquescent type of branching of the American elm; B, excurrent type of branching of the white spruce (*Picea canadensis*). (A, from photograph by G. J. Stout taken near Lock Haven, Penn.)

Monopodial and Sympodial Branching. As already indicated, the manner of branching of stems is closely related to the position of the buds. Since many of the buds are dormant, and since those which do develop, for various reasons, do not grow to the same extent, it follows that branches are not so regular in arrangement as are buds and leaves. The manner of branching of cultivated plants is often considerably altered by severe pruning.

In some woody plants the terminal buds begin to differentiate very early in the growing season and by autumn consist of a definite number of nodes and internodes, together with all the leaves that will be produced by this branch the following spring. In the horse chestnut (Fig. 56, *B*) the terminal buds may contain not only all the leaves produced by the branch but also the primordia of the bud scales of the next terminal bud. The actual elongation of such a stem takes place regularly, in a straight line, each year's growth being added as a direct continuation of the part of the stem already formed. Such growth is said to be **monopodial**. Lateral buds may give rise to branches in the same way. Sometimes a flower cluster is borne in the center of a terminal bud. When this happens, the development of the flowers and fruits brings the growth of the main branch to an end and the following year one or more of the lateral buds will develop into new side branches. Monopodial development occurs in the principal axis or trunk of evergreen trees with excurrent branching and in the branches of many deciduous trees with deliquescent or excurrent branching. Pine, spruce, fir, horse chestnut, and apple are examples. The first three have excurrent branching, the last two deliquescent branching.

In catalpa and other trees, a different type of development takes place (Fig. 56, *A*). None of the buds on stems of this type is very conspicuous, and the dormant buds are practically undifferentiated. The apex or tip of the stem consists of a mass of active meristematic cells which continue growth and the formation of nodes and internodes throughout the growing season. As a rule, the younger portions of the stem die at the end of the year, and the following season new growth proceeds from one or more of the lateral buds several nodes behind the apex. This manner of growth results in a series of short branches, each one attached to the side of the next preceding one, the whole forming an irregular or broken line. Often the dead portions of the branches persist for several years. This type of growth is called **sympodial**.

Annuals, Biennials, and Perennials. Plants are classified as **annuals**, **biennials**, and **perennials** depending upon the number of years they live, which in turn is often dependent upon the nature of the stems. **Annual** plants are those which arise from seed, mature, and die in one growing

season. Examples are bean, radish, and lettuce plants. Such plants generally have herbaceous stems. **Biennial** plants are those requiring 2 years to reach full development. During the first growing season, the seeds germinate, and the young plants develop usually a rosette of leaves and store up food in the roots for the following year's growth. During the second growing season, they reach maturity, produce flowers and seeds, and die. Examples of biennials are cabbage, beets, foxglove, and mullein. The stems of biennials are also of the herbaceous type. **Perennials** are plants which live for more than 2 years—in the case of some forest trees often for hundreds of years. In general, perennials are of two types, those with herbaceous stems and those with woody stems. The herbaceous type has aerial stems which die down to the ground each year and underground parts which live through the winter and the following growing season give rise to new shoots. Examples of these forms are asparagus, rhubarb, and many grasses. The woody types have aerial stems which live for many years. Each year a new season's growth is added to that already made, and the stem increases in diameter, largely by the addition of new wood. A detailed account of this growth is given in the following section on stem anatomy. Shrubs and trees are woody perennials.

ANATOMY OF STEMS

From what has been stated concerning the general diversity of form and manner of growth of stems it is not surprising that there is also great diversity of internal structure. In this respect the stems of dicotyledons differ from those of monocotyledons as well as from those of gymnosperms and lower vascular plants. Even in the dicotyledons, the internal structure of herbaceous plants is often quite different from that of woody plants, and the stems of vines are often unlike other stems. Within these larger groups there occur also many variations in arrangement and relative proportions of the tissues. In the discussion which follows, only a few representative forms are considered.

STEMS OF DICOTYLEDONS—PRIMARY TISSUES

Origin of the Tissues. If the extreme apex or tip of the stem is examined by cutting a thin section at right angles to the lengthwise axis and placing it under a microscope, it will be found to consist of cells that are all essentially alike (Fig. 61, I, A). There is but one tissue, the **promeristem**, or **primordial meristem**, which has persisted from the time when the whole plant was merely an embryo within the seed. The cells of the promeristem are parenchyma cells with large nuclei and dense cytoplasm (Fig. 60, B). If the stem is in an active, growing condition, many of these cells will be found dividing. Some of the daughter cells formed by these divisions

enlarge and divide again, causing the whole growing tip to expand and move forward. The cells at the extreme tip retain their meristematic condition, but most of those somewhat behind the tip sooner or later cease to divide and develop into permanent cells. If, therefore, a section is cut a short distance behind the tip, the cells will no longer be found to be all alike but several well-defined regions may be discerned (Fig. 61, I, *B*). In the stems of dicotyledonous plants there will be found a single layer of parenchyma cells, forming the outer extremity of the stem, called the **protoderm**; several groups or strands of smaller cells forming a circle as

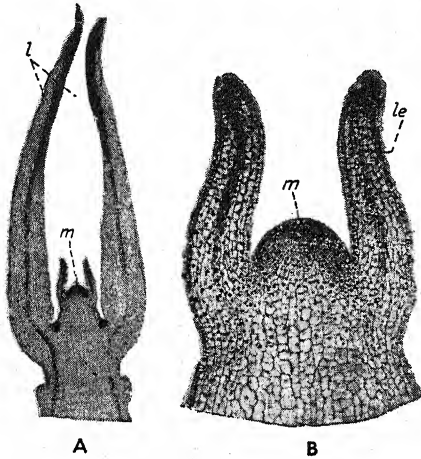


FIG. 60. Photomicrographs of lengthwise sections through the growing tip of *Coleus*, showing apical meristematic region of the stem. *B*, enlarged view of the terminal part of *A*; *l*, partly developed leaves folded over and protecting the primordial meristem, *m*; *le*, younger leaf.

seen in cross section, the **procambium** strands; and a mass of parenchyma cells filling in all the remaining space, called the **ground meristem**. These three regions constitute the **primary apical meristems**¹ and give rise, on further differentiation, to the **primary permanent tissues**. They are thus a transitional stage between the promeristem and the primary permanent tissues and may be considered simply regions of the apical meristem. All the cells of these regions, though showing some differentiation, are parenchyma cells and continue to divide, but the divisions occur less and less frequently until they cease altogether when the primary tissues are developed (Fig. 61, I, *C*). The protoderm

cells usually divide radially and thus continue to be a single layer of cells which becomes the **epidermis**. The procambium cells develop into the **vascular bundles**, consisting of xylem, cambium, and phloem. In some stems, the procambium gradually increases until it forms a complete cylinder, the outer layers of which become the **pericycle** and, in some stems, perhaps the **endodermis**. By some authors the endodermis is thought to be derived from the ground meristem. The ground meristem gives rise to the **cortex**, the **pith rays**, and the **pith**. In stems in which there are separate vascular bundles, the pericycle may also be considered

¹ For a discussion on meristems and their classification, the reader is referred to Chap. 9.

as arising from ground meristem. The epidermis, cortex, endodermis, pericycle, phloem, cambium, xylem, pith rays, and pith constitute the primary permanent tissues of the stem. They can be seen in a section cut just below the region of the primary apical meristems. They are called primary tissues because they are the first tissues formed from the meristem, and permanent tissues because they together form the primary permanent body of the stem which is complete in itself and capable of carrying out all the functions of the stem. Indeed, in the monocotyledons and in some of the lower vascular plants they are usually the only tissues developed. The primary permanent tissues may be defined as the tissues derived directly from the apical meristem. They are all developed by the transformation or differentiation of meristematic cells into permanent cells.

Arrangement of the Primary Permanent Tissues. In general, the primary permanent tissues of the stems of dicotyledons have a concentric arrangement (Figs. 61, I, C; 62). The pith, a mass of fundamental or parenchyma tissue, occupies the center of the stem. The vascular tissue is made up usually of separate vascular bundles, consisting of phloem, cambium, and xylem, and arranged in the form of a cylinder surrounding the pith and located between the pith and the cortex. The xylem of each bundle lies next to the pith and the phloem toward the cortex. The cambium, consisting usually of a single layer of cells that retain their meristematic condition and thus continue to divide, is located between the phloem and the xylem in each vascular bundle. The vascular bundles are separated from one another by radiating masses of parenchyma cells, called pith rays or medullary rays. The pith rays appear as extensions of the pith reaching out between the bundles toward the cortex. Surrounding the vascular bundles, and actually a part of the vascular system, is the pericycle, which, in stems, usually consists of several layers of cells. In some stems, an endodermis occurs immediately outside the pericycle. While the endodermis is a prominent tissue in roots, it is seldom seen in stems and even when it does occur usually does not have the well-defined structure it has in roots. The cortex lies external to the vascular bundles, forming a cylinder of fundamental tissue in the outer portion of the stem, in many respects resembling the pith. The epidermis consists of a single layer of cells surrounding all the other tissues and forming the outer protective layer of the young stem.

Structure of the Individual Tissues. It should be remembered that there are great diversities in the structure of the tissues of stems of dicotyledonous plants. Woody plants, herbaceous plants, and vines differ from one another and, in addition, each of these groups shows variations. It is, therefore, not possible to speak of a typical dicotyledon stem. Cer-

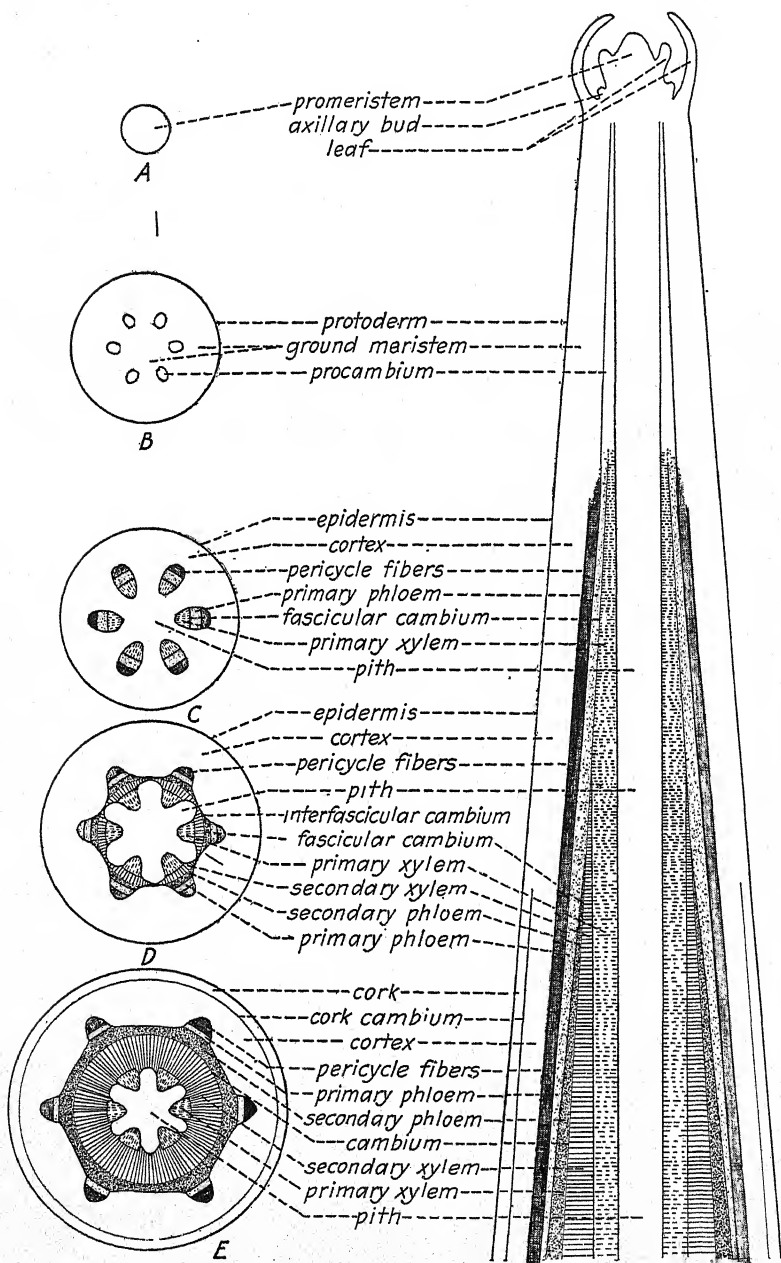


FIG. 61. I. Diagrammatic representation of the origin and arrangement of primary and secondary tissues in the stem of a dicotyledonous plant (modeled after a sunflower stem); longitudinal section of stem at right, transverse sections at different distances from the apex (A-E) at left. (Drawn by F. Brown.)

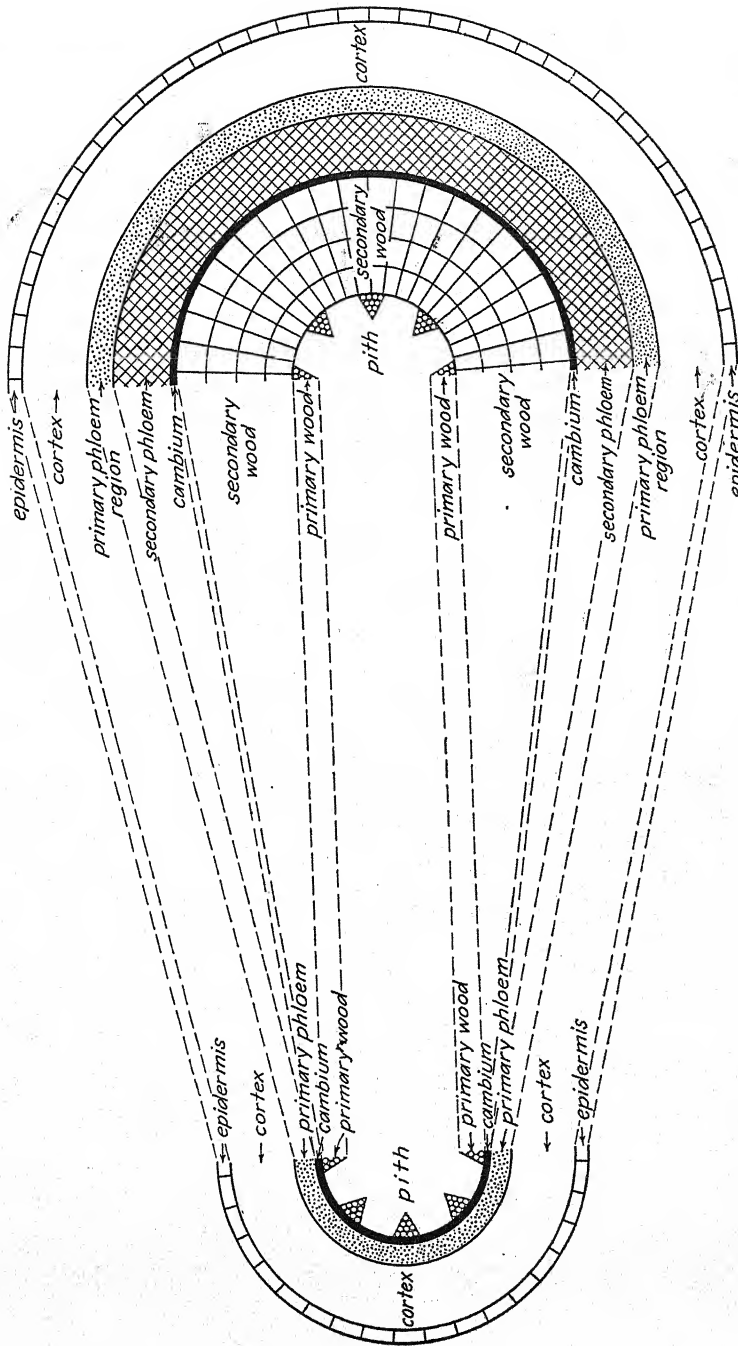
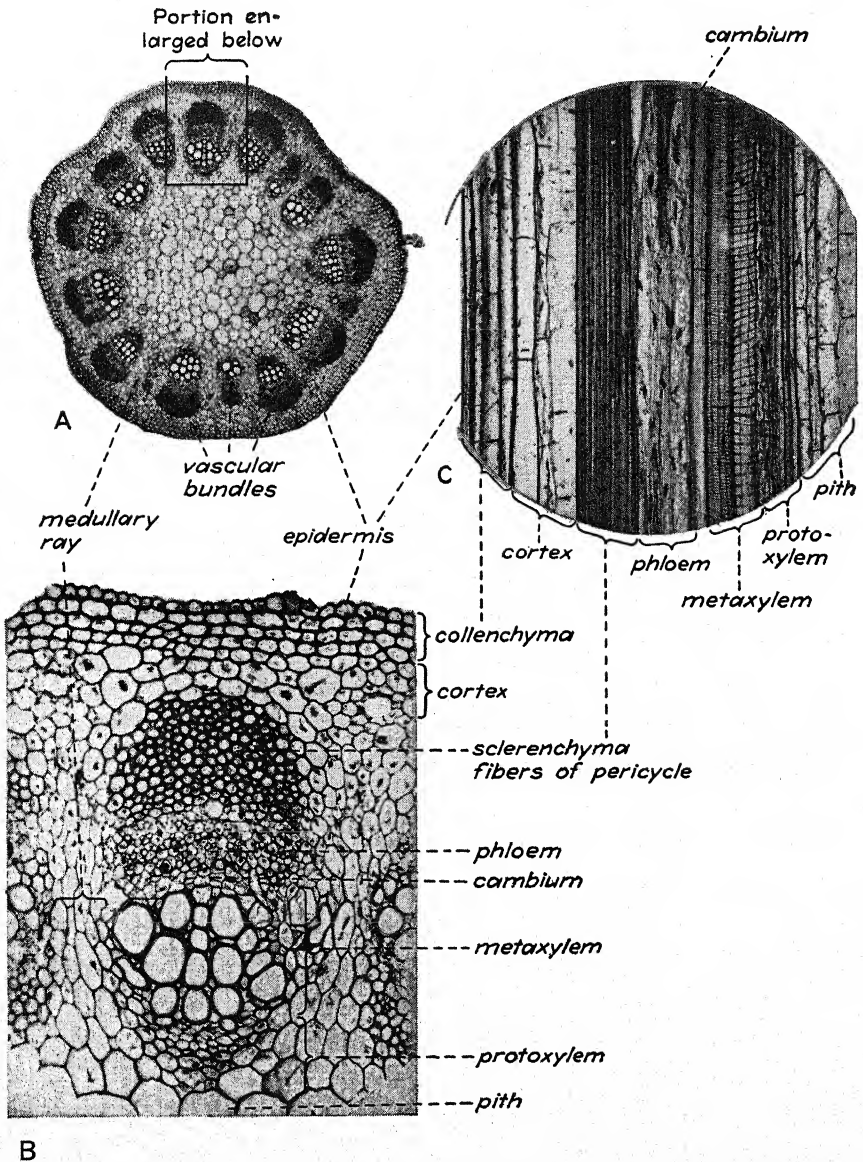


FIG. 61, II. Diagrammatic representation of the arrangement of primary and secondary tissues as seen in transverse sections of a stem of a dicotyledonous plant. Primary tissues at left; primary and secondary tissues at right.



B
 FIG. 62. The primary permanent tissues of the stem of a dicotyledonous plant, sunflower (*Helianthus annuus*). A, transverse section of entire stem, showing concentric arrangement of the tissues; B, enlarged portion of A, showing structure of the individual tissues, including one vascular bundle; C, enlarged median longitudinal section of A, from epidermis to pith and through the middle of a vascular bundle. (Photomicrographs by D. A. Kribs.)

tain structural features, however, are rather common. These are emphasized in the descriptions which follow.

The Epidermis. In general, the structure of the epidermis (Figs. 62; 63, A) of the stem does not differ greatly from that of the epidermis of other parts of the plant. It consists usually of a single layer of parenchyma cells, somewhat elongated in the direction of the lengthwise axis of the stem. The inner walls, lying next to the cortex, remain thin, while the outer walls that are exposed to air are thicker and usually cutinized. Many stomata are present, which, in woody plants, are later replaced

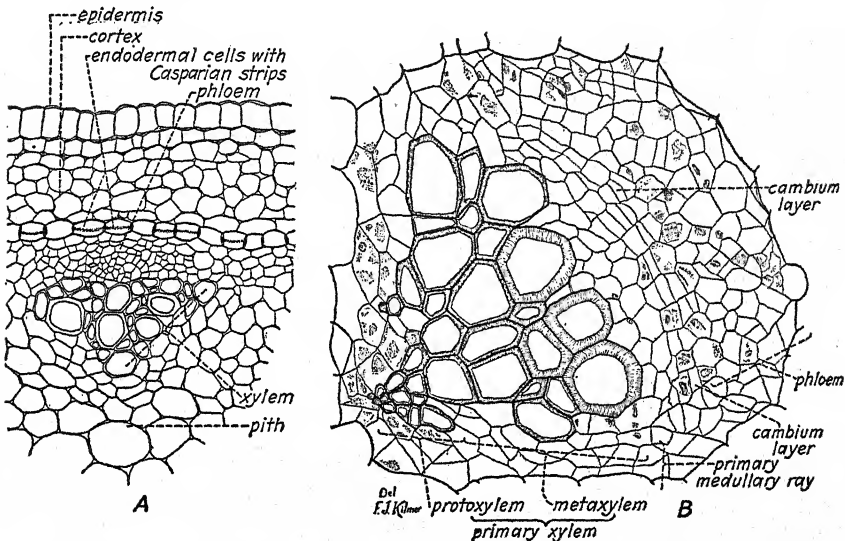


FIG. 63. A, portion of a transverse section through a young stem of nasturtium, showing a well-defined endodermis with Casparian strips and other primary permanent tissues; B, transverse section of a single vascular bundle of castor bean (*Ricinus communis*) showing the primary permanent tissues. (A, drawn by Helen D. Hill; B, by F. J. Kilmer.)

by lenticels. In such plants also, as the stem increases in diameter, the whole epidermis ultimately becomes broken and functionless.

The Cortex. The cortex (Figs. 62; 63, A) extends from immediately beneath the epidermis to the pericycle or to the endodermis, when this tissue is present. The outer part of the cortex next to the epidermis is usually made up of collenchyma cells, the walls of which are thickened at the corners as described on page 33. The collenchyma cells function in the support and strengthening of the young stems before this function is taken over adequately by the vascular tissues. The majority of the cells of the cortex are parenchyma cells, little differentiated, except in size, as compared with the meristematic cells from which they originate.

They are usually thin-walled and more or less rounded in shape, but may become angular through pressure. Sometimes, however, there are sclerenchyma cells present consisting of stone cells or fibers. The outer layers of the cortical cells frequently contain chloroplasts and hence carry on photosynthesis. Many of them are used for food storage.

The Endodermis. An endodermis, although common in roots and in the stems of most lower vascular plants, is seldom found in the stems of seed plants. A few types of dicotyledons, like nasturtium (*Tropaeolum*), however, have a well-defined endodermis (Fig. 63, A). When present, the endodermis forms the inner boundary of the cortex. It is composed of modified parenchyma cells and possibly has its origin in the fundamental-tissue system, although it is regarded by some authors as part of the vascular system. The walls of the endodermal cells are frequently heavily thickened and the radial walls suberized. Characteristic thickenings on the walls occur in strips, called Casparian strips. The cells sometimes contain an abundance of starch. The exact function of the endodermis in the stem is not well known, but, from the fact that it is so often absent, it may be assumed that it is not so important a structure in the stem as it is in roots.

The Pericycle. In the stems of many dicotyledonous plants the pericycle is difficult to recognize because of its similarity in structure to the cortex and because of the frequent absence of an endodermis in stems. In roots, it will be recalled that the pericycle is often a single layer of cells lying immediately inside the well-defined endodermis and hence stands out more prominently. In stems there are usually several layers of pericycle cells. They may consist of only parenchyma or of both parenchyma and sclerenchyma. When sclerenchyma is present, it is most often made up of fibers which may appear in groups lying just outside the phloem of the vascular bundles (Fig. 62) or between the phloem of adjacent bundles. Sometimes these fibers form a continuous or an irregular band around the vascular tissue (Fig. 64). The sclerenchyma fibers may be lignified, as in hemp, or consist largely of cellulose, as in flax. They serve as strengthening elements in a young stem. As mentioned in Chap. 3, they are of considerable economic importance in such plants as hemp and flax, being used in making thread, twine, and rope.

The parenchyma of the pericycle resembles the parenchyma of the cortex, pith, and other regions of the plant and functions primarily as a food-storage tissue. In many stems the pericycle consists entirely of parenchyma cells.

The Vascular Bundles. In most herbaceous stems and in many woody stems of dicotyledonous plants, the procambium strands very early differentiate into separate vascular bundles consisting of phloem, cambium, and

xylem (Fig. 62). Separate bundles may not be formed, in which case concentric sections of these three tissues are developed. The phloem of each vascular bundle lies next to the pericycle and the xylem next to the pith, with the cambium between. In some dicotyledonous plants, like members of the cucumber and nightshade families, another section of phloem is found in each vascular bundle next to the pith, *i.e.*, between the xylem and the pith. Bundles of this type, in which phloem occurs on both sides of the xylem, are called **bicollateral bundles**, while those in which there is only one section of phloem are called **collateral bundles**. In the bicollateral bundle, cambium is ordinarily found only between

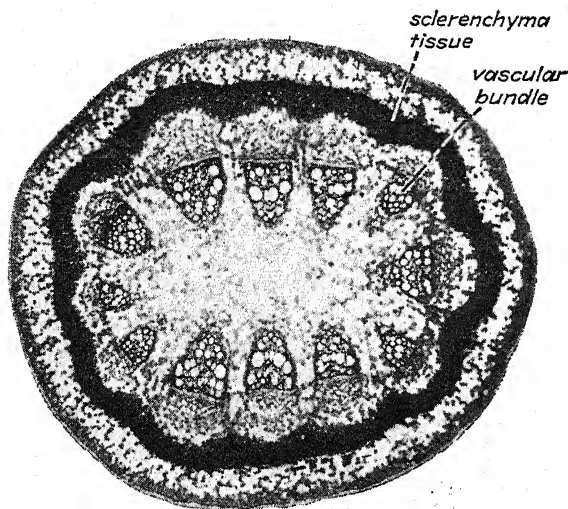


FIG. 64. Transverse section of stem of *Aristolochia*, showing continuous ring (or section of cylinder) of sclerenchyma fibers outside the ring of vascular bundles.

the outer phloem and the xylem. The collateral bundle is the usual type in dicotyledonous plants.

The *phloem* of each bundle (Fig. 63, *B*) consists of sieve tubes, companion cells, phloem parenchyma, and often fibers. Each of these types of cells has already been described on page 37. A sieve tube and its companion cell are usually sister cells formed from the same procambium cell. Often the companion cell divides again, transversely, forming two or more companion cells adjacent to a sieve tube. Originally the sieve tube has a nucleus and cytoplasm but, as the cell matures, only the cytoplasm remains. Cytoplasmic strands can often be seen extending from one sieve-tube cell to another through the sieve plates forming the end walls. The companion cells, even at maturity, have both nucleus and

cytoplasm. The sieve tubes are the food-conducting channels of the stem. Phloem parenchyma is largely used for food storage.

The *cambium* (Fig. 63, *B*) is usually a single layer of cells lying between the phloem and the xylem and retaining its meristematic condition. The cambium cells thus retain their ability to divide. They are thin-walled cells, rectangular as seen in cross section, but considerably elongated in the direction of the lengthwise axis of the stem. They usually have a prominent nucleus and dense cytoplasm. By the division of the cambium cells, new cells are added to the phloem and the xylem, giving rise to secondary tissues described later.

The primary *xylem* (Figs. 63, *B*; 65) of the stems of dicotyledonous plants consists of tracheids, vessels, or tracheae, wood fibers of various kinds, and xylem parenchyma. It will be recalled that the tracheids and vessels are chiefly water-conducting cells, the tracheids also functioning in support. In very young primary xylem, the vessels are usually of the ringed or spiral type (Fig. 13, *A-D*). Ringed or spiral vessels are usually formed during a period of rapid growth, when the vessels are being stretched by the rapid elongation of the stem. Vessels formed after the stem has ceased rapid elongation are more likely to be of the scalariform or pitted types (Fig. 13, *E, F*). In pitted vessels and other conducting cells, there are thin areas in the walls, called pits. These pits sometimes have overhanging borders, in which case they are called bordered pits (Fig. 79, *F*).

The wood fibers of the xylem are greatly elongated cells with small cavities or lumina and thick, hardened walls. The end walls taper and often overlap with the ends of the cells above and below. They are the principal strengthening elements of the xylem of dicotyledons, the overlapping of the cells assisting materially in this function. The thickening of the wood fibers as well as that of tracheids and other xylem elements consists of cellulose and lignin or lignocellulose. For this reason, such cells are said to be lignified.

The xylem parenchyma consists of living cells that have not been differentiated into other xylem elements such as fibers and vessels. These cells can be recognized by the presence of square or horizontal ends, generally not tapering, and by their protoplasmic contents. The walls of most xylem parenchyma cells are somewhat thickened but not to the extent of those of other xylem elements. The chief function of the xylem parenchyma is food storage.

The first xylem to be differentiated from the procambium strands usually lies next to the pith. This xylem is the **protoxylem** (Figs. 63, *B*; 65). Its cells are usually smaller in diameter than those of the xylem later developed. The balance of the xylem formed from the procambium strands

gradually differentiates from the protoxylem toward the cambium and phloem. This xylem is the **metaxylem** (Figs. 63, B; 65). The cells of the metaxylem are not only larger but also thicker walled than the protoxylem,

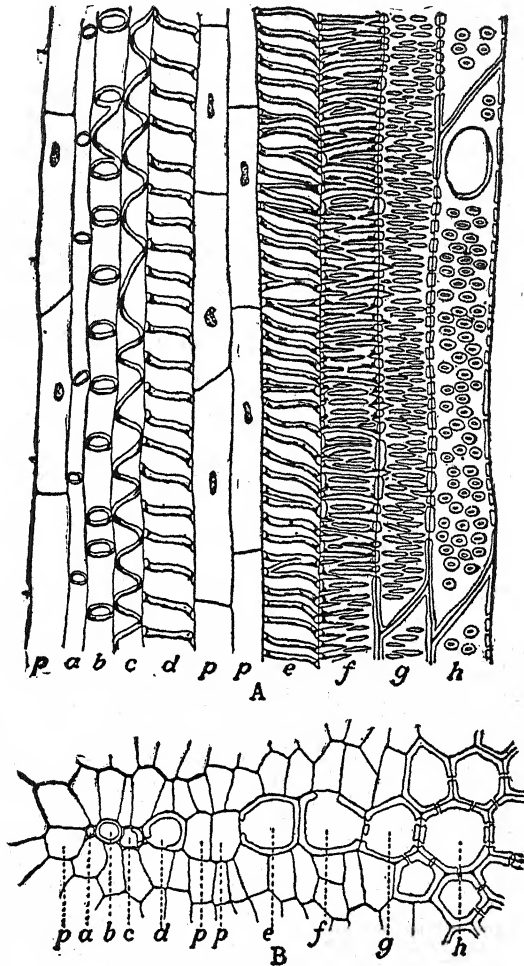


FIG. 65. Protoxylem and metaxylem in transverse, B, and longitudinal, A, section in *Lobelia*; a, b, annular elements; c, d, e, spiral elements; f, scalariform element; g, scalariform-reticulate element; h, pitted vessel; p, parenchyma cell. (From A. J. Eames and L. H. McDaniels, "An Introduction to Plant Anatomy," McGraw-Hill Book Company, Inc., New York, 2d ed., 1947.)

being more heavily lignified. The protoxylem and the metaxylem together constitute the primary xylem, both of them having been derived directly from the procambium strands. It will be recalled that, in the

root, the protoxylem is laid down next to the pericycle and that the metaxylem develops in a direction toward the center of the root, gradually forming a solid core of xylem, a condition called **exarch**. In the stem of dicotyledons, the direction of development of the metaxylem is directly opposite, *i.e.*, away from the center of the stem, and is spoken of as an **endarch** condition, the term endarch meaning "inner origin." The primary phloem may also be differentiated into **protophloem** and **metaphloem**, but since there is never as much phloem developed as there is xylem and since the cells of the protophloem and metaphloem are more nearly alike, it is usually not possible to distinguish between them. The protophloem lies next to the pericycle and the metaphloem next to the cambium.

Pith and Pith Rays. The pith (Figs. 62; 63, A) is composed of fundamental parenchyma cells located in the center of the stem inside the vascular cylinder. In general, the pith does not undergo great modification, although in a few instances the tissues are so greatly altered that their relation to fundamental tissue is difficult to recognize. This is true of the large central storage tissue of the potato tuber. The pith cells are usually rather large in comparison with the cells of the ground meristem from which they are derived and are frequently interspersed with numerous air spaces. Their chief function is food storage. In older stems the pith often disintegrates and is finally lost.

In all stems of dicotyledons in which there are separate vascular bundles, masses of parenchyma cells extend between the bundles from the pith to the pericycle. These masses of cells appear as extensions of the pith, out between the bundles, and are known as pith rays, or medullary rays (Fig. 62). In structure and function they are similar to the pith cells.

Lactiferous Ducts. In a number of families of dicotyledons, as well as in a few families of monocotyledons, there is a much branched system of tubes or ducts in which a milky sap called **latex** is found. This system usually runs all through the plant from roots to leaves and is even found in fruits. It is often especially abundant in the cortex and pith and is found in secondary tissues as well as in the primary permanent tissues. Two types of lactiferous ducts are found, **latex vessels** and **latex cells**. The latex vessels originate in rows of meristematic cells, the end walls of which become dissolved and absorbed much as xylem vessels are formed. The latex vessels, however, remain living and have many nuclei; *i.e.*, they are coenocytic. These vessels are connected by many branches, forming an anastomosing system which usually extends all through the plant. This type of system is found in the poppy family (Papaveraceae), the chicory family (Cichoriaceae), the banana family (Musaceae), and a few others including the para rubber tree (*Hevea brasiliensis*), which is the chief commercial source of rubber.

The so-called "latex cells" are also long tubes, but they are, in reality, single cells which originate as minute structures in the embryo, or young plant in the seed, and as the plant grows they elongate and branch, keeping pace with the growth of the plant until they form a branching system extending throughout the entire plant body. This type of duct system is found in members of the milkweed family (Asclepiadaceae) (Fig. 66), in the spurge family (Euphorbiaceae), and in several others.

Latex is a white, yellow, orange, or red viscous fluid, usually an emulsion, consisting of proteins, sugars, gums, alkaloids, enzymes, oils, salts, and other substances. The latex of a number of plants is collected and used in making a number of commercial products, among the most important of which are rubber, chicle, opium, and papain.

The function of latex in the plant is not well understood, but it is thought to be connected in some way with the nutrition of the plant and perhaps to be important in healing wounds and protecting wounded surfaces from attacks of parasites and from drying out.

Familiar examples of plants bearing latex are common lettuce, the milkweeds, the house rubber plant (*Ficus elastica*), and the wild bloodroot (*Sanguinaria canadensis*).

Summary of the Primary Permanent Tissues. At the extreme tips of the stems of dicotyledons there occur masses of undifferentiated, dividing cells called promeristem or primordial meristem. As the stem elongates, the meristem differentiates into three well-defined regions known as the protoderm, the procambium, and the ground meristem. These three meristematic regions, on further differentiation, give rise to the primary permanent tissues of the stem. The protoderm gives rise to the epidermis, the procambium to the vascular bundles consisting of phloem, cambium, and xylem, and the ground meristem to the cortex, pith, pith rays, and possibly to the pericycle and the endodermis, although these last two tissues, in some stems at least, probably arise from procambium. The primary permanent tissues together constitute the primary plant body,

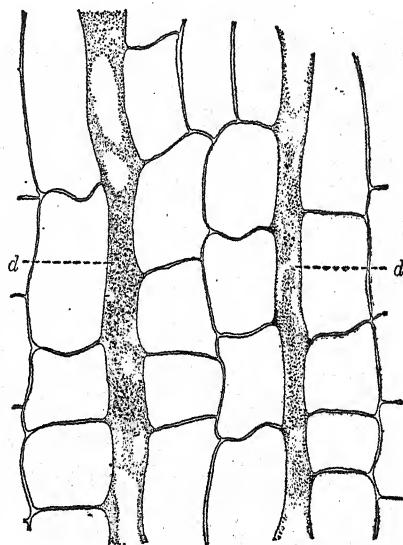
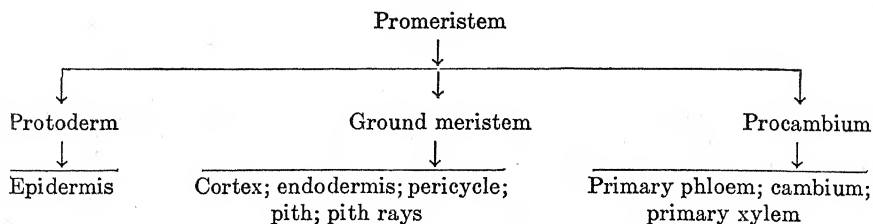


FIG. 66. Lactiferous ducts, *d*, of the latex-cell type, as seen in a longitudinal section of the cortex of milkweed. (Drawing by F. Brown.)

which is a complete entity in itself. The origin and composition of the primary tissues are summarized in the accompanying diagram.



STEMS OF DICOTYLEDONS—SECONDARY TISSUES

The development of the primary permanent tissues causes the stem to grow in length and to some extent in thickness. It gives rise to the primary plant body and to most of the branches of the main stem. In the majority of dicotyledons, and especially in woody plants, growth in diameter is brought about chiefly by the development of **secondary tissues**. Secondary tissues it will be recalled are those derived from the activity of cambium or from tissues already fully differentiated. There are two principal types of secondary tissues found in the stems of dicotyledonous plants, *viz.*, **secondary vascular tissues** and **periderm**. Each of these is considered separately.

SECONDARY VASCULAR TISSUES

The Cambium Cylinder—Fascicular and Interfascicular Cambium. After the primary permanent tissues have been formed and sometimes even before they are fully differentiated, the secondary tissues of the vascular cylinder begin to develop. In stems in which there are separate vascular bundles a complete cambium cylinder is often first developed. This is brought about by the formation of **interfascicular cambium** between the original vascular bundles and continuous with the **fascicular cambium** which is the original cambium of the bundle formed directly from the procambium strands. The interfascicular cambium arises in a row of cells lying between the vascular bundles in the region where the pith rays meet the pericycle (Fig. 67). These cells begin to divide tangentially and with the fascicular cambium form a complete cylinder of cambium around the stem. In many stems of dicotyledons and especially in woody stems, a complete cambium cylinder is developed from the original procambium strands, although not all parts of this cylinder may be developed simultaneously. When fully developed, this cambium cylinder consists of a single layer of cells, appearing as a circle in cross section and intersecting each of the vascular bundles, when separate bundles are present, between the primary phloem and the primary xylem. The new cells formed by the

division of the cambium differentiate into secondary xylem, which becomes continuous with the primary xylem, and secondary phloem, which becomes continuous with the primary phloem. These additions to the phloem and xylem cause the stem to increase in diameter (Fig. 61, I, II).

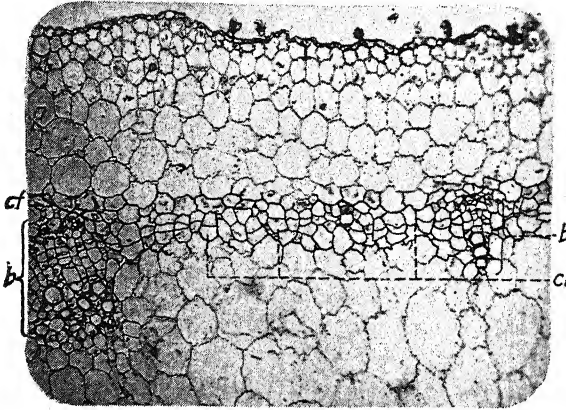


FIG. 67. Portion of mint stem, in transverse section, showing development of interfascicular cambium; *b*, primary vascular bundles; *cf*, fascicular cambium; *ci*, interfascicular cambium, accentuated by drawing over the cell outlines on the photomicrograph. The fascicular cambium and the interfascicular cambium together form a complete cylinder within the stem.

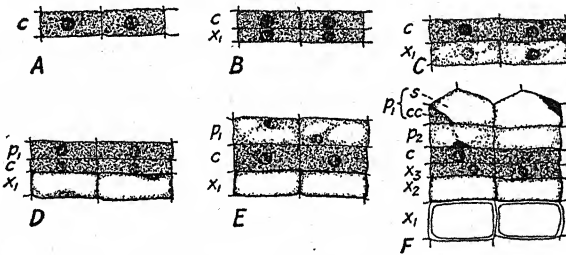


FIG. 68. Semidiagrammatic representation of the origin of secondary xylem and phloem from the cambium. A-F, successive stages; A, cambium cells; B, division of the cambium, and C, enlargement of the daughter cells, the upper ones remaining cambium and the lower ones beginning to differentiate into xylem, x_1 ; D, the cambium has divided again, cutting off cells, p_1 , which will become phloem; E, beginning of differentiation of the phloem, p_1 ; F, three further divisions of the cambium have taken place, resulting in the formation of the xylem cells, x_2 and x_3 , and the phloem cells, p_2 ; in the meantime, each of the cells, p_1 , has divided again and cut off a companion cell, cc , the remaining daughter cell s , becoming a sieve tube. (Drawing by F. Brown.)

The individual cambium cells, as previously stated, are elongated in the direction of the lengthwise axis of the stem but appear rectangular in cross section, the tangential axis being the longer. Cambium cells usually divide along the tangential axis. When a cambium cell divides, one of the daughter cells becomes, on differentiation and perhaps on further division,

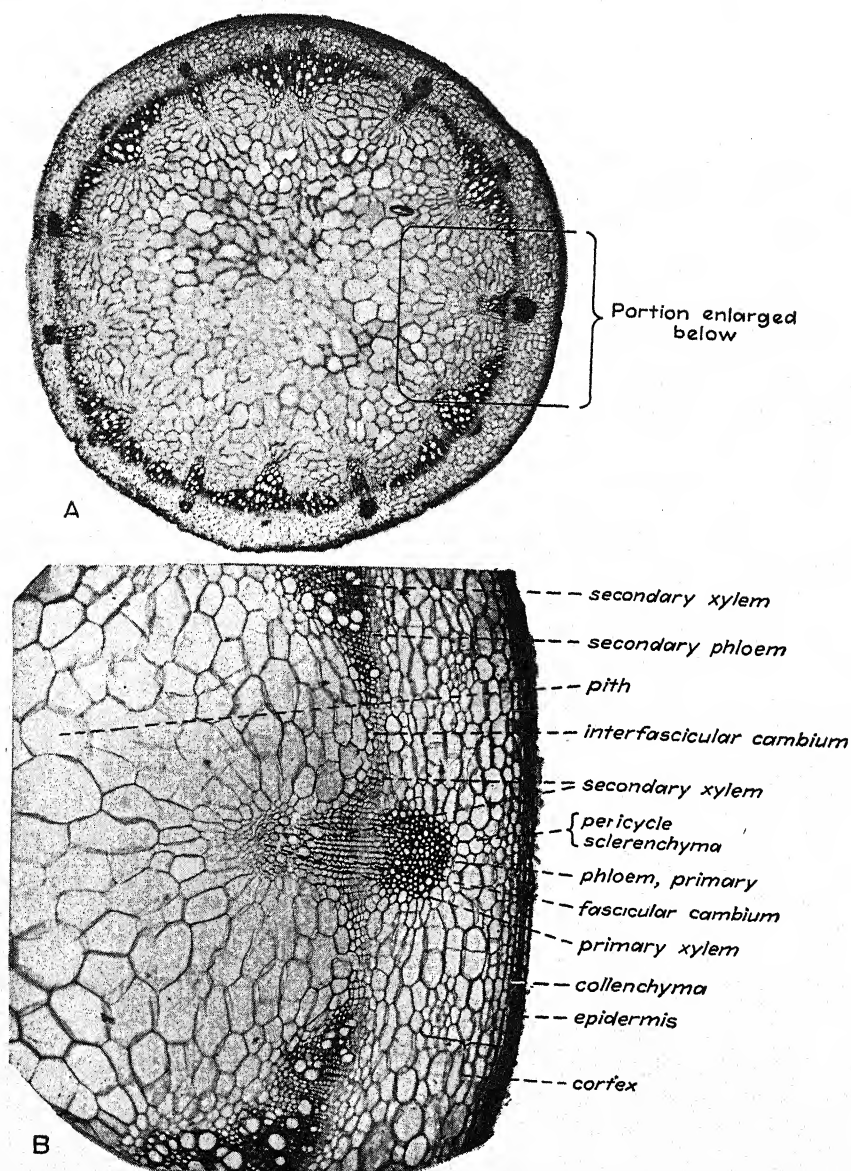


FIG. 69. I. Secondary tissues in the stem of sunflower (*Helianthus annuus*); A, transverse section of the entire stem showing beginning of development of secondary tissues as they are added to the primary tissues; B, enlarged view of a portion of A.

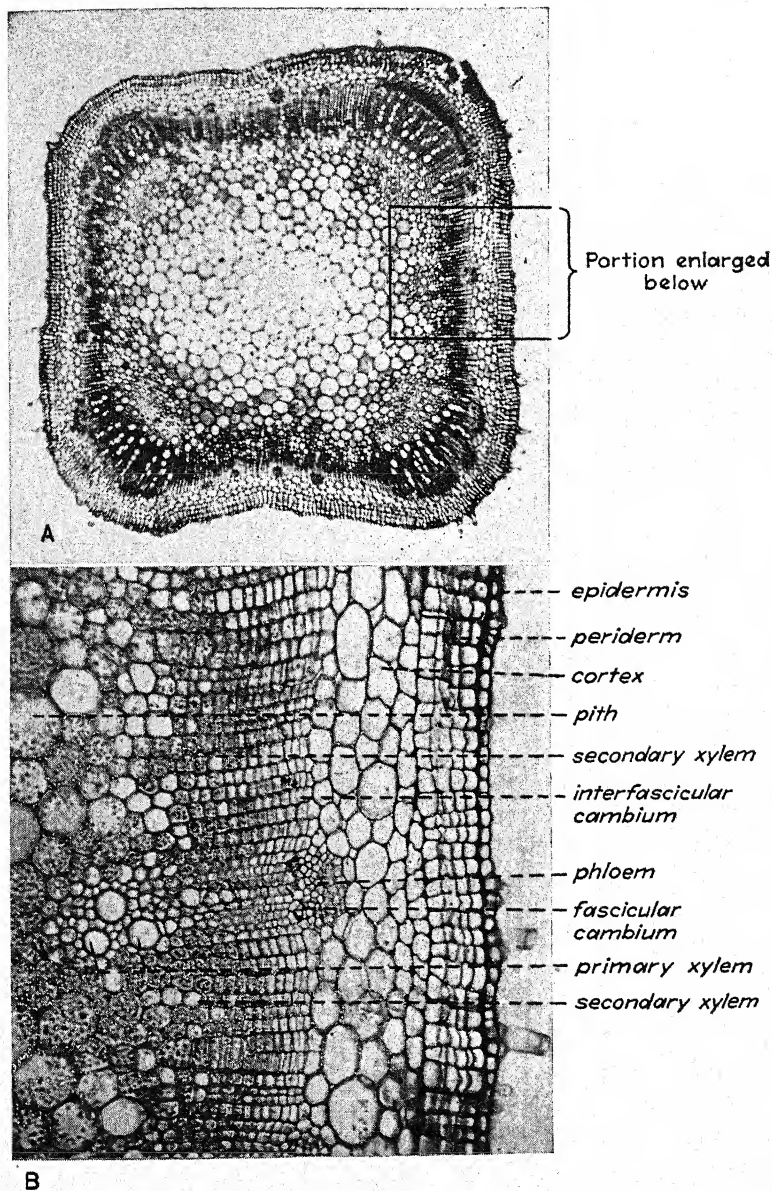


FIG. 69, II. Secondary tissues in the stem of a mint; A, transverse section of the entire stem showing periderm and a complete cylinder of secondary vascular tissue; B, enlarged view of a portion of A.

permanent xylem or phloem, while the other daughter cell retains its meristematic condition. In this way the cambium cylinder perpetuates itself (Fig. 68). In some of the oldest trees, the cambium cylinder has thus remained active for a thousand years or more, giving rise to new secondary tissues each year.

Secondary Phloem. If the daughter cells of the cambium which lie next to the phloem become permanent cells, they develop into secondary phloem. Ultimately, this secondary phloem, together with the primary phloem, forms a complete cylinder of phloem surrounding the cambium cylinder (Fig. 69, II). The secondary phloem, like the primary phloem, may consist of sieve tubes, companion cells, phloem parenchyma, and fibers (Fig. 70). A sieve tube and companion cell may be formed from the same initial cell. Secondary phloem usually resembles the primary phloem to such an extent that it is not possible to determine where one begins and the other ends. Furthermore, there is no marked difference, ordinarily, in the size of the cells or the relative proportions of the different cell types formed during different seasons of the year. Hence, the yearly additions of phloem cannot be determined so readily as can the yearly additions of xylem, described below. As the stem grows older, however, the primary phloem, as well as some of the older secondary phloem, is pushed outward and placed under greater and greater strain because of the increasing circumference of the stem resulting from cambial activity and the addition of new layers of wood, so that ultimately this phloem may become torn and functionless. The phloem, as well as all the tissues outside the phloem, is constantly being forced outward along with the cambium as new cells are added by the divisions of the cambium cells. The youngest phloem always lies nearest the cambium.

Secondary Xylem. By far the greater number of cells resulting from the division of cambium become differentiated into xylem. This means that the daughter cells of the cambium lying next to the xylem more often become the permanent tissues, while the other daughter cells remain cambium. These cells differentiate into secondary xylem, which becomes continuous with the primary xylem and with it forms a complete cylinder, as does the phloem. The secondary xylem soon comes to make up the bulk of the vascular tissue of woody stems.

The kinds of cells composing the secondary xylem (Fig. 71) are, in general, the same as those of the primary xylem, but the types of vessels formed and the relative proportions of vessels, tracheids, and wood fibers are often quite different. Great variations also exist among different species as to the relative proportions of these different elements formed. The great differences in appearance of different kinds of wood are partly explained by these differences. In some species, vessels predominate, while in others

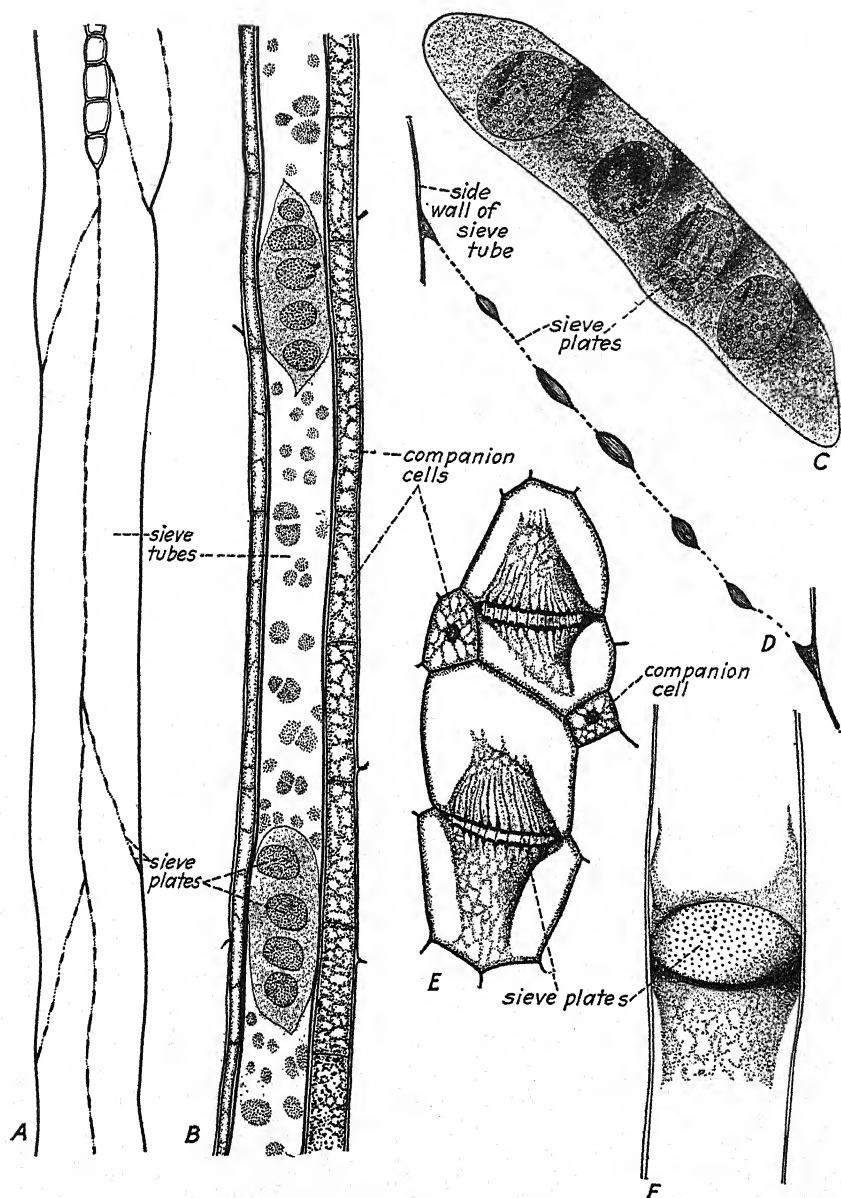


FIG. 70. Secondary phloem tissues. *A*, tangential view of sieve-tube segments; *B*, radial view, showing sieve plates in both vertical and inclined walls; *C*, radial view of inclined end wall of sieve tube, showing four sieve plates; *D*, end of sieve-tube segment cut tangentially, showing six sieve plates; *E*, transverse section of sieve tubes and companion cells, showing sieve plates on side walls of sieve tubes; *F*, radial view of ends of two adjacent sieve tubes, showing a single horizontal sieve plate. All taken from *Liriodendron*.

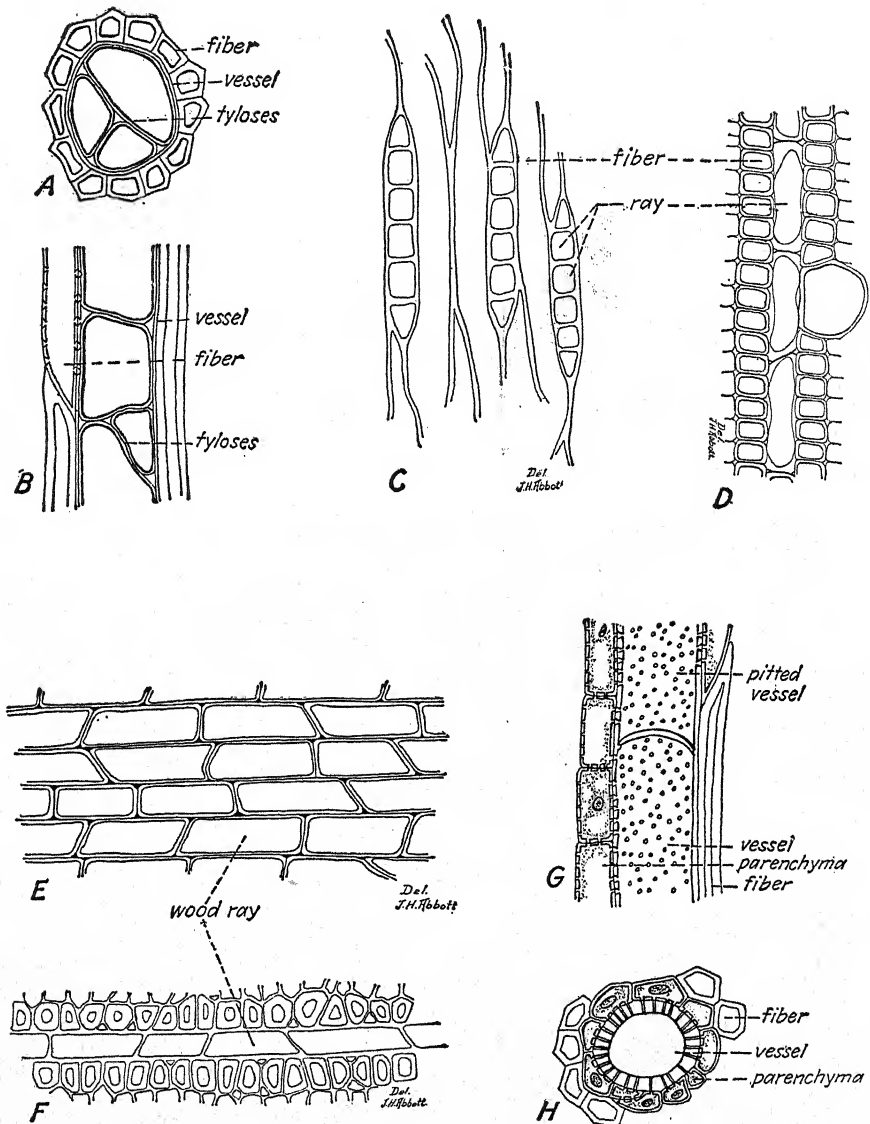


FIG. 71. Secondary xylem tissues. A, transverse section; B, longitudinal section of oak wood showing wood fibers and vessels, the vessels containing tyloses; C, tangential, and D, transverse, view of birch wood, showing diffuse rays and wood fibers; E, radial, and F, transverse, views of wood rays in tanbark oak; G, longitudinal, H, transverse, view of wood of ash, showing vessels surrounded by parenchyma and fibers. (Drawings A, B, G, and H by Robert T. Quick; C, D, E, and F by Marian A. Sutch.)

there are larger masses of thick-walled wood fibers. In general, the vessels of the secondary xylem are chiefly of the scalariform or pitted type. The walls of the tracheids and wood fibers are usually also much thicker than those of these elements in primary xylem. The entire mass of secondary xylem usually has a much more regular organization than does the primary xylem.

Wood Rays and Phloem Rays. A prominent feature of the secondary xylem of most dicotyledons is the development of **wood rays** (Fig. 72). These consist of rows of living parenchyma cells usually containing storage foods and running radially through the xylem. Like the other xylem elements, they are formed by the division of cambium cells. In some cases, they may extend from the cambium to the pith. In other cases, they may begin with any year's development of xylem. They also extend into the phloem and are sometimes there referred to as **phloem rays** (Fig. 72). They originate in the cambium and, once started, usually continue to develop through all the secondary xylem and phloem later formed by additions of cells from the cambium. They are like thin ribbons of tissue extending radially from the center toward the periphery of the stem. While each one does not extend very far vertically up and down, they are usually so thoroughly distributed through the xylem that any given cell is only a few cells at most away from a wood ray. Wood rays should not be confused with the primary pith rays previously mentioned. Wood rays, originating in the cambium, are entirely secondary tissues.

Annual Rings. One of the most conspicuous features of the secondary xylem, as viewed in cross section, is that it appears as a series of concentric layers (Fig. 73, A-C). These layers are not always uniform in width around the stem but may be much wider in one place than in another. Each layer represents a year's addition to the xylem and is commonly called an **annual ring**. The width of an annual ring depends upon the amount of xylem made in the particular year. Each annual ring is made up of two parts, an inner layer of **spring wood** and an outer, usually more compact, layer of **summer wood**. The difference between these two parts is brought about by the fact that the tissues formed in the spring, when growing conditions are more favorable, are usually different in cell size, cell type, and cell arrangement from those formed later in the year. In many stems, vessels predominate in the spring wood and the cells generally are larger in diameter. In the summer and especially toward the end of the growing season, the cells do not become so large, are more compact, and often thicker walled. There are often more wood fibers developed in the summer wood. Toward the end of the season the cambium ceases to divide and goes into a resting condition over winter. On the resumption of favorable growing conditions in the spring the cycle is repeated. It is this alternation of

active growth and rest and the difference between spring growth and summer growth which cause the yearly increments of xylem to stand out as annual rings. The age of a stem may be determined by counting these rings, although occasionally false annual rings may be formed by one cause or another, such as drought, defoliation by insects, and other causes.

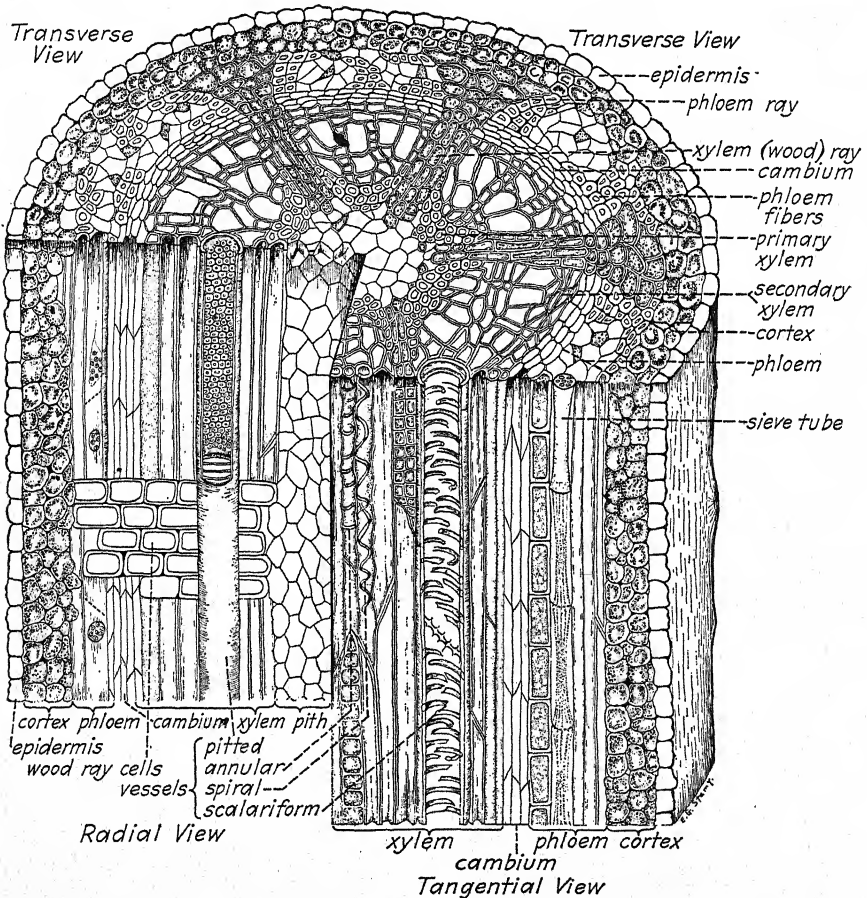


FIG. 72. Semidiagrammatic representation of a one-year-old stem of *Liriodendron*, in transverse, radial, and tangential views. (Drawing by Edna Stamy Fox.)

While there is a similar increment of phloem each year, the annual increments do not stand out as rings because there is relatively less phloem formed each year and because there is not so marked a difference in the cells formed during the different periods. It should be mentioned that, even during the first year of growth of a woody plant, much of the

wood consists of secondary xylem. The first annual ring, therefore, is made up of all the primary xylem as well as the first year's secondary xylem.

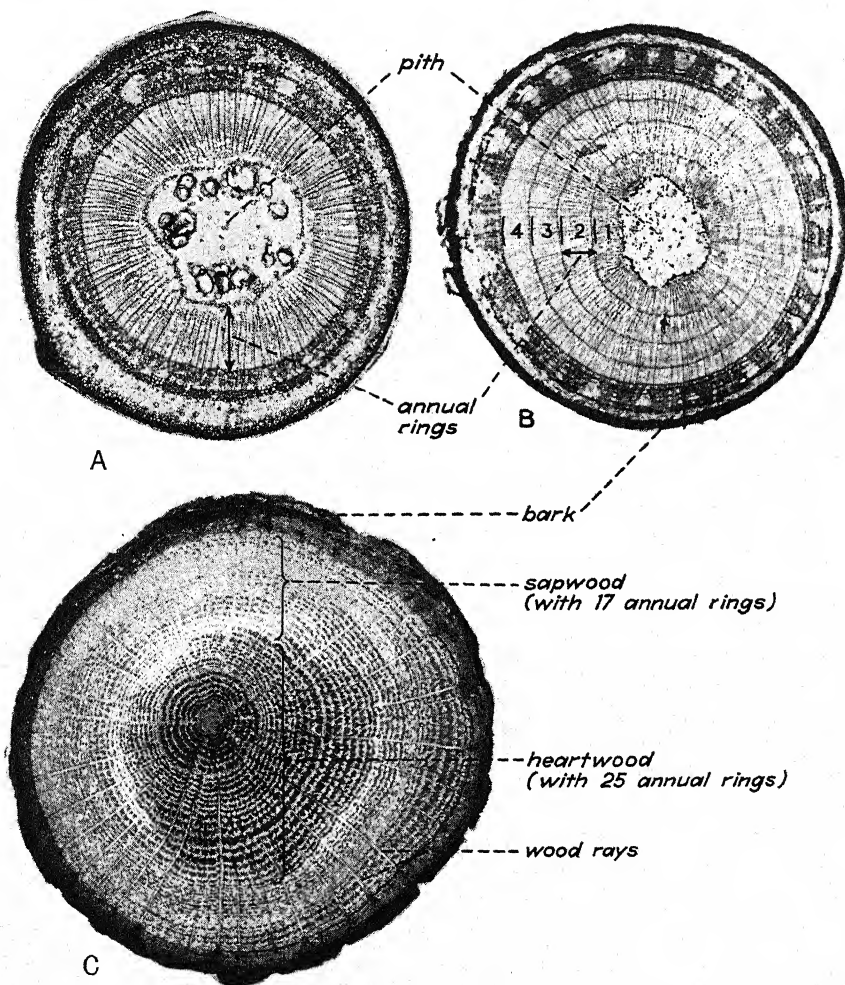


FIG. 73. Transverse sections of woody stems of dicotyledons showing annual rings of xylem. A and B, photomicrographs of *Tilia* stems, A enlarged more than B; A, one year old; B, four years old; C, transverse section of a branch of oak showing annual rings, wood rays, bark and wood, heartwood and sapwood. (Photomicrographs A and B by D. A. Kribs; C photographed by Homer Grove.)

Sapwood and Heartwood. In many stems the youngest or latest formed xylem comprising only a few years' growth functions most actively in conduction and food storage. This wood is called **sapwood** (Fig. 73, C).

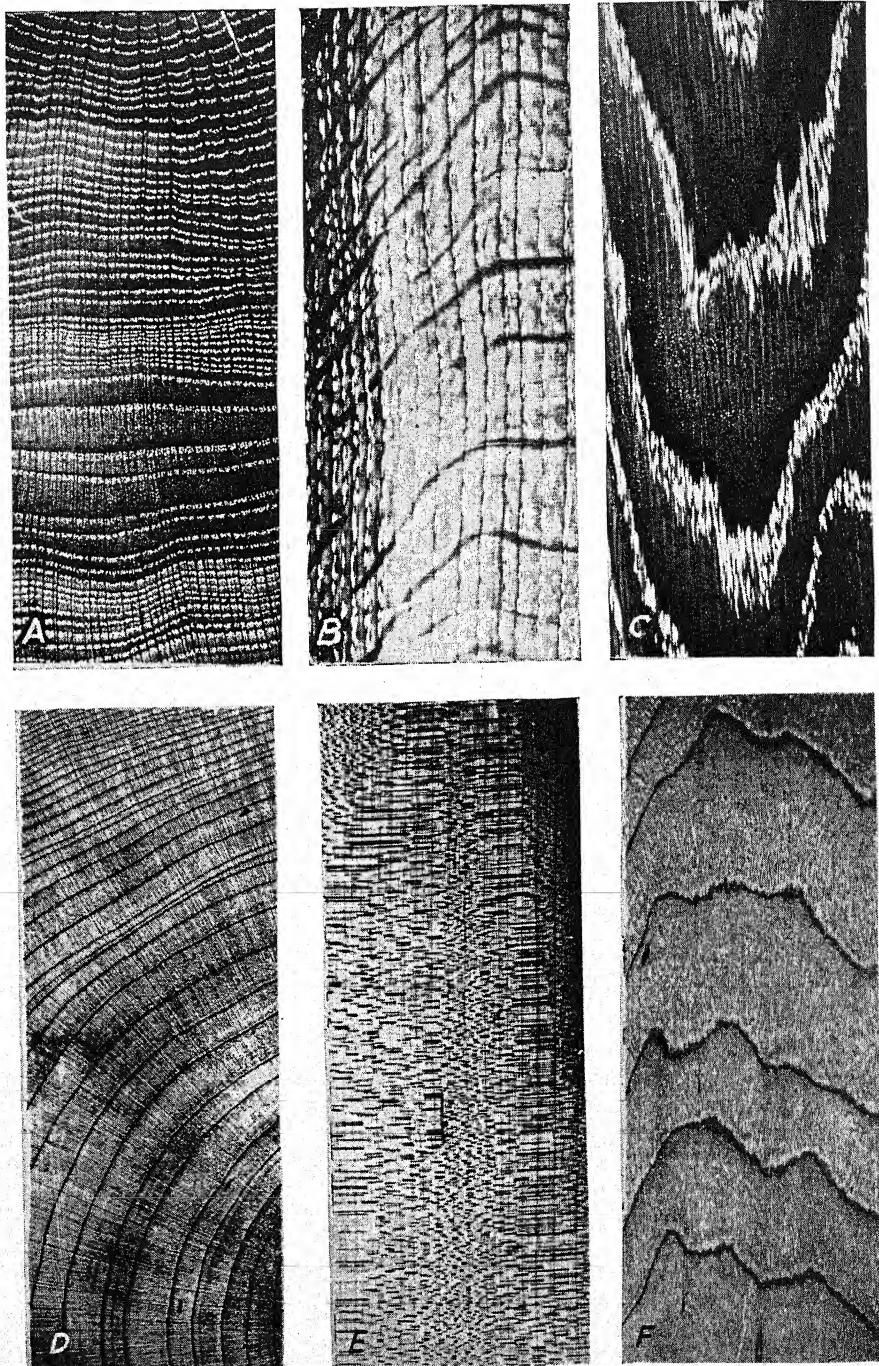


FIG. 74. Appearance of wood in different sections. A-C, yellow oak (*Quercus Muhlenbergii*) wood. A, transverse section; B, radial section; C, tangential section; D-F, silver maple (*Acer saccharinum*) wood; D, transverse section; E, radial section; F, tangential section.

It often has a much lighter color. The older wood sometimes becomes stained through the deposition of oils, resins, and coloring matters, and the cavities often become clogged through deposits of gummy materials and tyloses, which interfere with conduction. Such xylem is called **heartwood**. In some species the heartwood dries out, while in others it remains wet. In still other species the entire xylem continues to function. Heartwood is usually more durable as timber than sapwood and in general is commercially more valuable than sapwood. Both sapwood and heartwood are made up almost entirely of secondary xylem, the primary xylem having become altogether insignificant in amount in a tree old enough to show these regions.

Appearance of Wood in Different Sections. When the xylem or wood is viewed in **transverse** or **cross section** (Figs. 74, *A, D*), the annual rings, as previously mentioned, stand out in concentric layers. The wood rays cross these layers, forming lines running radially from the center toward the circumference. The vessels often appear as large pores, while the wood fibers and tracheids form smooth, compact regions made up of smaller, thick-walled cells. Spring wood and summer wood can usually be distinguished without difficulty. If a small section of a large tree is examined in cross section, the annual rings are approximately parallel to each other, with the wood rays crossing them at right angles.

In a lengthwise **radial section** (Fig. 74, *B, E*), *i.e.*, one cut along a radius of the stem, the annual rings appear as parallel bands which differ in different kinds of wood. The wood rays in this section are cut lengthwise and appear as broad bands running across the lengthwise axis. The individual cells of the wood rays appear brick-shaped in striking contrast to the ordinary xylem elements, most of which are greatly elongated in the direction of the lengthwise axis of the stem. Annual rings are readily discernible. Quarter-sawn lumber is cut radially. It is chiefly the position of the wood rays that gives such lumber its striking appearance.

In a lengthwise **tangential section** (Fig. 74, *C, F*), *i.e.*, one cut at right angles to a radius of the stem, the annual rings often appear as irregular figures. In this section, the wood rays are cut in transverse section and hence appear as short chains of parenchyma cells running in the direction of the lengthwise axis or with the lengthwise axes of the other xylem elements. The individual vessels, tracheids, and wood fibers appear much as they do in the radial section.

THE PERIDERM

As the secondary tissues begin to form in the vascular cylinder, another type of secondary tissue starts to develop in the cortical region, which is an adjustment to the increase in diameter of the stem from within. In some

herbaceous plants the epidermis and the outer cortical cells may continue to increase in size and number of cells for some time and thus keep pace with the increasing diameter. In most woody plants, however, sooner or later

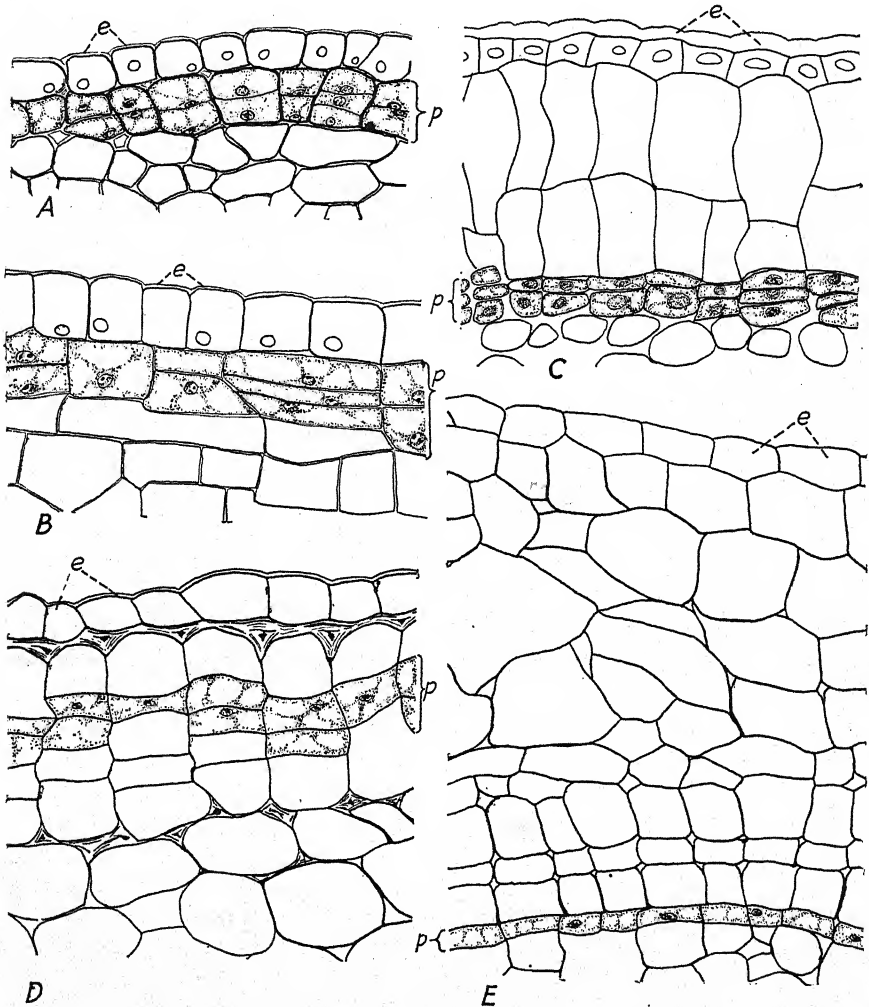


FIG. 75. Origin of phellogen and development of periderm. A, transverse section, and B, longitudinal section of outer portion of stem of ash, showing origin of phellogen in the layer of cells immediately beneath the epidermis; C, transverse section of *Magnolia* stem, showing periderm layers; D, mint stem, showing periderm; E, *Fuchsia* stem, showing origin of phellogen in inner cortex; e, epidermis; p, phellogen.

the epidermis ceases to function and a new tissue, the **periderm**, develops. The periderm, as in roots, consists of three layers, viz., a meristematic layer called the **phellogen**, or **cork cambium**, the **phellem**, or **cork layer**, formed

external to the phellogen, and the **phelloderm**, formed inside the phellogen next to the cortex (Fig. 75).

The Phellogen. The phellogen always arises from living cells that are already mature. In the majority of stems of dicotyledons it arises from a single layer of cortical cells located immediately beneath the epidermis (Fig. 75, A, B). In some plants, like the apple, it arises in the epidermis itself, and in others in deeper lying cortical cells. It will be recalled that in the root the phellogen usually arises in the pericycle. Most of the divisions of the phellogen cells are along the tangential axis. One of the daughter cells remains phellogen, and the other develops into permanent tissue. If the latter happens to lie toward the periphery of the stem, it forms phellem or cork, and if it lies toward the inside of the stem it forms phelloderm. As a rule, in stems, much more cork is formed than phelloderm.

The Phellem. The cells of the phellem or cork are very compact and at maturity, nonliving. Their walls contain the waterproof material suberin, which tends to prevent the inner tissues of the stem from drying out. In a cross section of the stem, cork cells often appear roughly rectangular in shape, similar to the phellogen cells but somewhat larger. It is from the phellem of a species of oak (*Quercus suber*) that the cork of commerce is obtained.

The Phelloderm. The cells of the phelloderm remain living cells not unlike ordinary cortical cells. They sometimes function in photosynthesis and in food storage. In many stems relatively little phelloderm is formed.

Lenticels. In older stems the periderm completely replaces the epidermis as a protective covering. The suberized cork cells of the phellem act as a moistureproof covering for the living tissues of the stem. Since this layer is also more or less impervious to gases, gaseous exchange between the exterior and the interior of the stem would be very difficult were it not for the development of lenticels already mentioned. These structures are usually developed from the phellogen, immediately beneath places in the epidermis where stomata occur (Fig. 76). The phellogen in such places develops, instead of cork, a mass of loose, thin-walled parenchyma cells with many air spaces. These often protrude through the epidermis and project slightly above the outer surface of the stem, appearing as small dots or ridges, which have already been described.

Duration of the Periderm. In some plants, the periderm, as just described, persists for many years, adding new cork layers each year. It is obvious, however, that, since the cork cells are dead, there is a limit to the extent to which they can stretch to keep pace with the internal expansion of the stem. In many trees, the outer layers are soon broken and separated. Often entirely new periderm layers develop deeper in the stem. These may be formed first in the inner cortex, then in the pericycle, then in the phloem, and finally in the secondary phloem. In old tree trunks the ma-

jority of the periderm layers are developed in the secondary phloem and all the tissues on the outside become greatly broken and split up, making a very irregular, ridged outer surface such as that occurring on oak trees. The primary permanent tissues outside the vascular cambium cylinder thus become entirely functionless and in many cases are sloughed off altogether and lost. It is obvious that all tissues outside the functioning phellogen are cut off from the internal food and water supply and therefore die.

Bark and Wood. In all woody stems one or more years old, two well-defined regions can be discerned in cross section, the **bark** and the **wood** (Fig. 73, C). The bark comprises all the tissues outside the vascular cambium cylinder and therefore includes, in younger stems, the periderm, the cortex, the pericycle, the primary phloem, and the secondary phloem. In older stems all the primary tissues are usually so disorganized as to be unrecognizable, the major tissues being periderm and secondary phloem. The wood, on the other hand, includes all the xylem, primary and secondary, the primary xylem being preserved near the center of the stem. In some stems a third zone of pith may still be discernible, but in most old woody stems, and especially in trees, the pith occupies so small a portion of the complete cross section as to be hardly visible or it may be completely disintegrated.

STEMS OF GYMNOSPERMS

Much of the discussion that has been given concerning the origin and development of the primary permanent tissues of dicotyledons is equally applicable to the stems of gymnosperms, such as the pines, firs, and spruces. Like the stems of dicotyledons, the stems of gymnosperms have a concentric arrangement of the primary permanent tissues, with separate vascular bundles consisting of phloem, cambium, and xylem. The secondary tissues also arise in the same way as they do in dicotyledons. The chief difference between these kinds of stems is in the types of cells in the xylem and the phloem. The xylem of the gymnosperms (Figs. 77 to 79) is made up almost entirely of tracheids with bordered pits on the radial walls. In a transverse section, these tracheids appear rather thick-walled and roughly square in shape. The xylem is traversed by many thin wood rays (Figs. 77, 78). In many species there are rather conspicuous resin ducts (Figs. 78, 79) which run both radially and longitudinally through the stem, but in other species resin ducts are entirely lacking. These resin ducts, or canals, are lined with parenchyma cells and are used for the secretion and conduction of resin. Little or nothing is known of the function of this resin to the plant. The xylem contains neither vessels nor wood fibers, and in some species even the xylem parenchyma is lacking (Fig. 78). Annual rings are found (Fig. 77), caused by the difference in size of tracheids formed in the

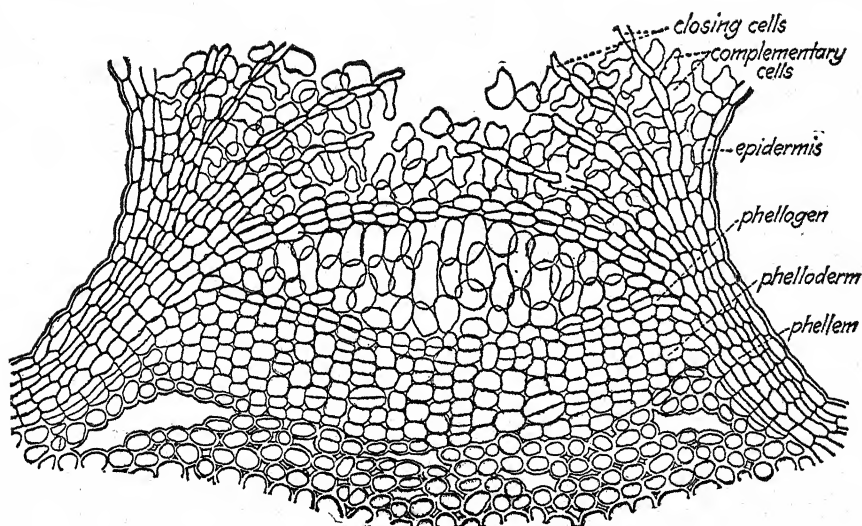


FIG. 76. Lenticel of *Prunus avium* in transverse section of stem. A number of successive layers of complementary and closing tissue have been formed, and the large amount of phelloderm dips inward into the cortex. (After Devaux, from A. J. Eames and L. H. McDaniels, "An Introduction to Plant Anatomy," McGraw-Hill Book Company, Inc., New York, 2d ed., 1947.)

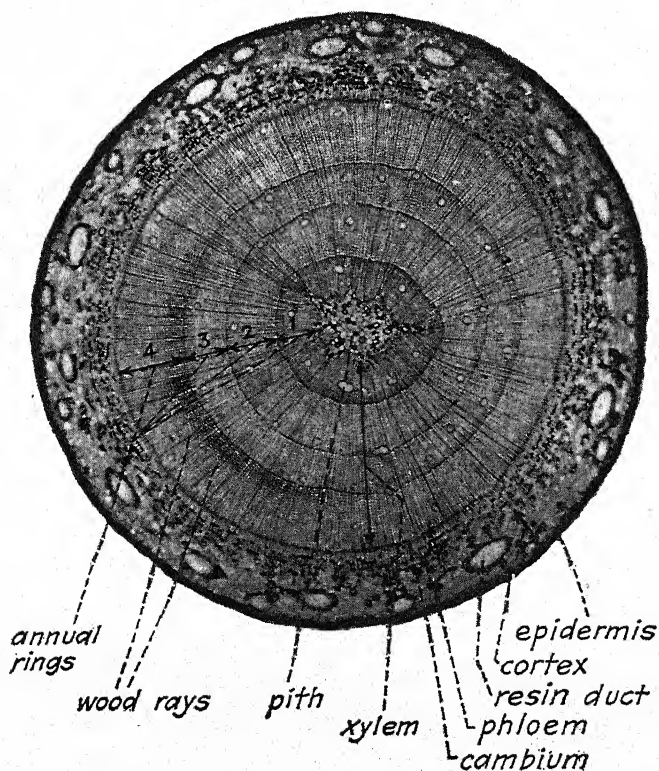


FIG. 77. Transverse section of the stem of pine, four years old, showing annual rings (1-4) and other tissues.

spring as compared with those formed in the summer. Another conspicuous feature of gymnosperm stems is the complete absence of companion cells in the phloem. Sieve tubes with sieve plates on the side walls, however, are abundant (Fig. 79, *B*). In general, the gymnosperms have

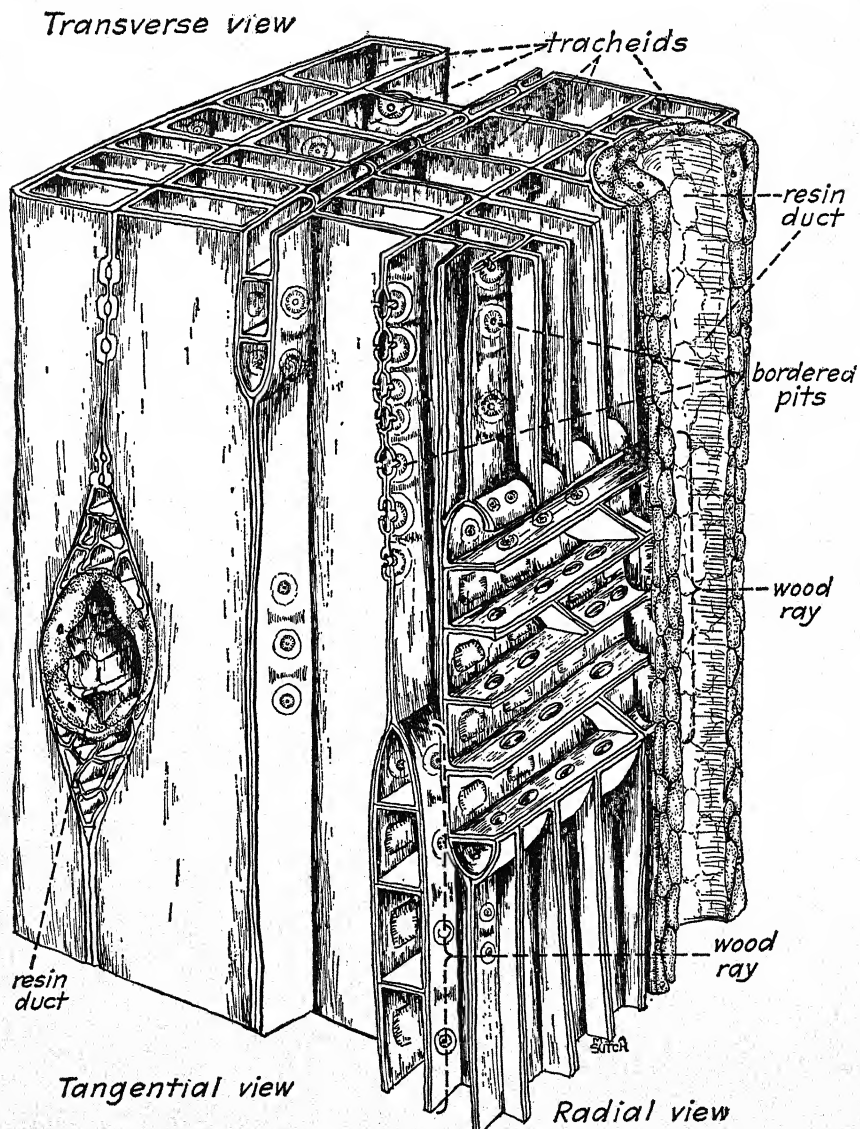


FIG. 78. Semidiagrammatic representation of a small block of white-pine wood as seen in transverse, tangential, and radial views. (Drawing by Marian A. Sutch.)

woody stems. Many of them attain great age and enormous size, like the giant redwoods and firs of the Pacific Coast and the cypress of the South. In these large trees the development of secondary wood is enormous in quantity. The conifers as a whole are among the most important forest trees used for timber.

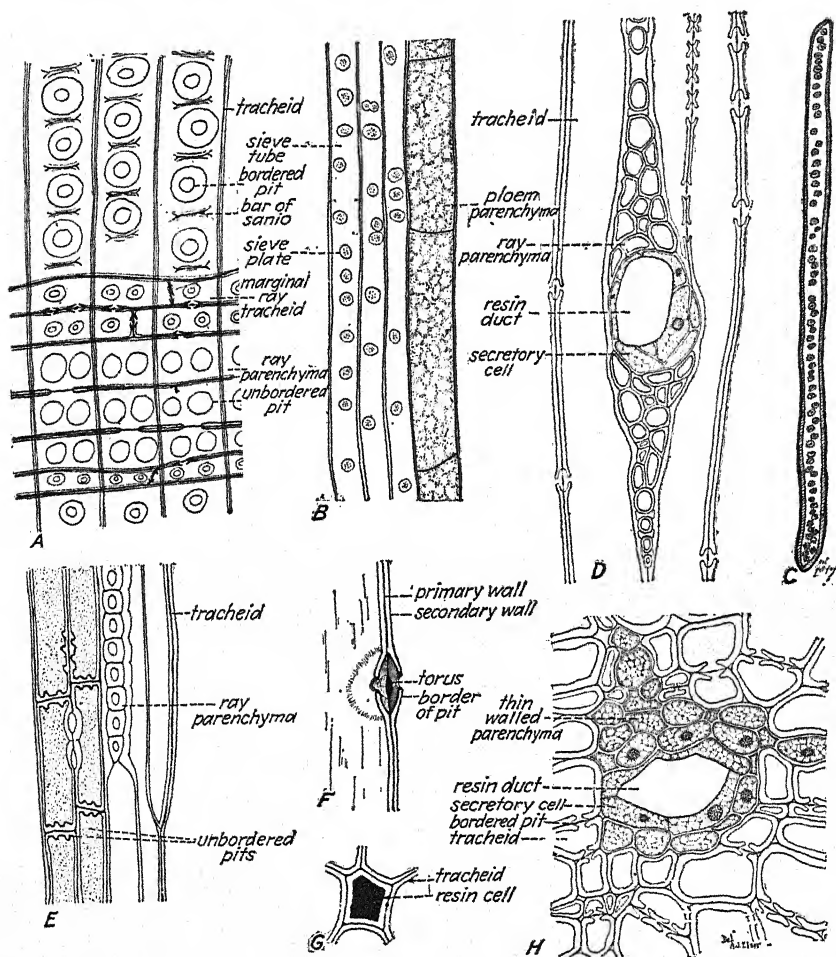


FIG. 79. Xylem and phloem elements in gymnosperm stems. A, radial section of pine wood, showing tracheids running vertically and a wood ray running horizontally; B, phloem from pine stem; C, radial view of a tracheid with bordered pits; D, tangential view of ray with horizontal or radial resin duct; E, tangential section of *Taxodium* wood; F, diagram of a bordered pit; G, transverse view of a resin cell of *Sequoia* with adjacent tracheids; H, transverse view of a resin duct with surrounding cells. (A drawn by R. M. Gerfin; C by J. W. Holli-day; D and H by A. J. Elser; E by M. A. Sutch; F and G by R. T. Quick.)

STEMS OF MONOCOTYLEDONS

The stems of monocotyledons are, in general, made up entirely of primary permanent tissues derived, as in dicotyledons, from apical meristems. In many monocotyledonous plants, however, and especially in the grasses,

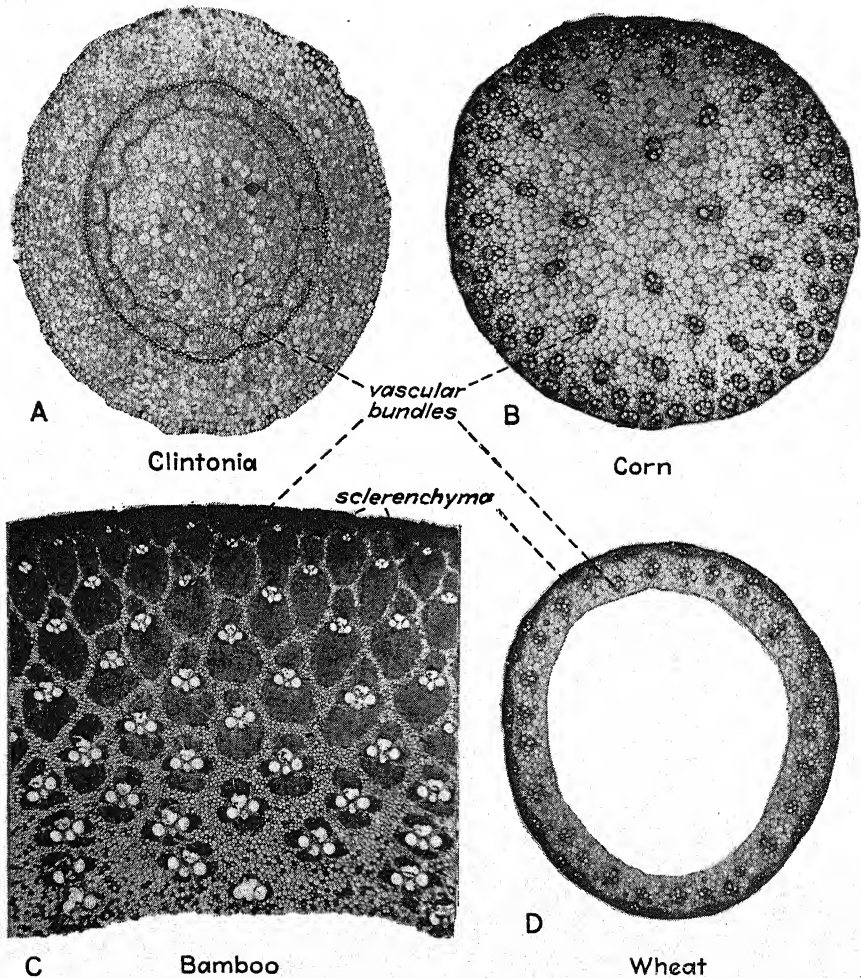


FIG. 80. Photomicrographs of transverse sections of stems of monocotyledons showing arrangement of vascular bundles. (Photomicrographs by D. A. Kribs.)

upright stems do not elongate much until the time of flowering, when a rapid development of the stem takes place, producing flowers at its summit. In this growth, the development of the primary permanent tissues of the nodes frequently lags behind that of the internodes, with the result that

meristematic regions (of the nodes) alternate with regions in which permanent tissues have already been fully differentiated (in the internodes). These meristematic regions of the nodes are called **intercalary meristems**. Intercalary meristems are quite generally found in all growing regions of monocotyledons. Ultimately these meristems are completely transformed into permanent tissues. In the stems they occur only at the nodes (several to many) nearest the tip (Fig. 53, B).

In general, the stem of the monocotyledons consists of a mass of fundamental tissue very much like the pith of the dicotyledons, with isolated vascular bundles which pass vertically through this fundamental tissue (Fig. 80). An epidermal layer covers the outside of the stem. In many monocotyledon stems a tissue consisting of several layers of hardened, thick-walled sclerenchyma forms a cylinder just beneath the epidermis.

The essential structural features of monocotyledon stems are the arrangement of the bundles, the structure of the individual bundle, and, in general, the lack of cambium. In contrast to the concentric organization of tissues common in the dicotyledons, most of the monocotyledons have a "scattered" arrangement of the vascular bundles, like that of corn (*Zea mays*) (Fig. 80, B). In others, however, the bundles are grouped in the central portion of the stem; as in the rhizome of the so-called "calamus root" or "sweet flag" (*Acorus calamus*). In this rhizome an endodermis-like structure surrounds the central region. In *Clintonia* the bundles are close together and grouped in a definite cylinder or ring (Fig. 80, A). The stems of certain monocotyledons, like wheat and some other grasses, at maturity have hollow centers (Fig. 80, D).

The individual bundles of the monocotyledon stem vary in structure with the several genera. The bundles vary also in structure in the different parts of the plant and those of the internode frequently differ from those of the node of the stem. The bundle of the rootstock of *Acorus calamus* (Fig. 81, A) is a typical **concentric** bundle. In this bundle the phloem is located in the center, as a core. The phloem consists of sieve tubes and companion cells and a considerable amount of undifferentiated parenchyma. A thin cylinder of xylem tissue, consisting mostly of vessels, surrounds the central phloem core. The organization of phloem in the center, surrounded by xylem, constitutes the **amphivasal** type of concentric bundle. This type of bundle structure is frequently found in the underground stems of those types of monocotyledons possessing rhizomes. It is not characteristic of the aerial stems of monocotyledons of the grass type, although it may occur in the internodal regions of these plants.

In the internodes of the stems of cereals, such as corn and wheat, and in other grasses, another type of bundle occurs. In this case, the phloem is not surrounded by the xylem but is located toward one side of the bundle,

generally the side toward the circumference of the stem. The phloem consists of sieve tubes and very distinct companion cells of small diameter which usually are square in cross section. The xylem is located adjacent to the phloem and usually on the side toward the center of the stem. The vascular tissues, therefore, assume the collateral organization (Fig. 81, *B*). The xylem consists of ringed, spiral, and pitted vessels, some fibers, and parenchyma. Frequently in this type of bundle a cavity is formed in the parenchyma just inside the xylem tissues. This is due to rapid growth and the separation of some of the cells, leaving a large intercellular space.

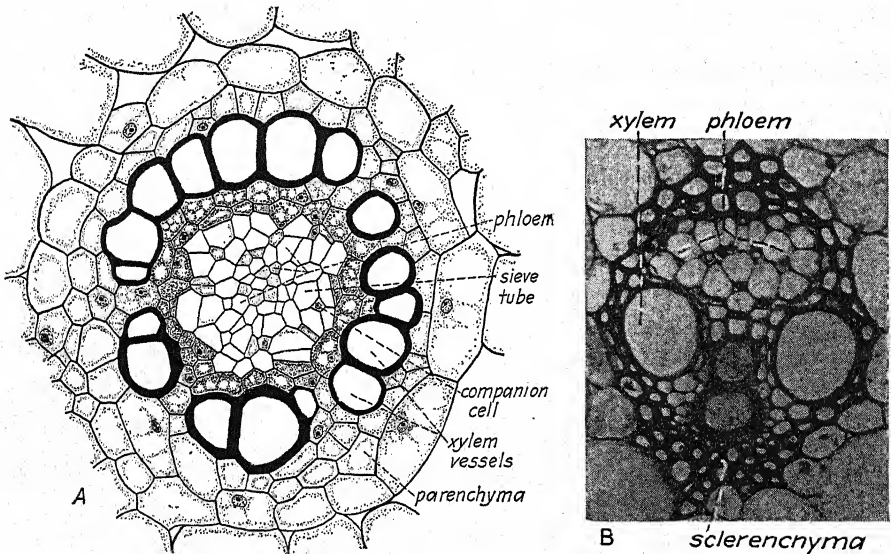


FIG. 81. *A*, amphivasal bundle of *Acorus* showing structure of the bundle with phloem surrounded by xylem; *B*, collateral bundle of corn.

Usually there is a layer of sclerenchyma tissue, several cells in thickness, more or less completely surrounding the bundle. In many types of monocotyledons this bundle sheath is rather thick. This is particularly true in the bamboo (Fig. 80, *C*) where the many bundle sheaths of sclerenchyma form an important strengthening tissue of the plant. Bundles of the monocotyledons have no cambium layer and, therefore, cannot continue growth as do the dicotyledons. Bundles lacking cambium are called "closed" bundles, meaning that they are closed to indefinite growth.

Typically, cambium is absent in monocotyledon stems, and secondary growth, therefore, does not occur. In these cases, the whole plant is composed of primary tissues differentiated from the primary apical meristems and the primary intercalary meristems located in the regions of the nodes

and near the bases of leaves. A few monocotyledons, however, have a feeble cambium which develops in the fundamental stem tissues and gives rise to a small amount of atypical secondary tissue. Many monocotyledons show traces of vestigial cambium in the bundles. Such cambium is functionless. True interfascicular cambium is absent in monocotyledons.

TYPES OF STELES FOUND IN PLANTS

The term **stele** is applied to the vascular skeleton of the plant or to the vascular tissue as a whole. A number of different types of steles are found in plants, depending upon the relative positions of the different tissues and particularly the positions of the xylem and phloem with respect to each other. These are the **radial stele**, the **protoste**, the **ectophloic siphonostele**, the **amphiphloic siphonostele**, and the **dictyostele**.

The Radial Stele. The radial stele (Figs. 82, A; 83, A) consists of a solid (star-shaped in cross section) central mass of xylem, with pointed radiating arms extending radially toward the pericycle. The protoxylem forms the pointed arms of the xylem and the metaxylem occupies the center of the stele. The phloem lies between the radiating arms, occupying radii that alternate with those of the protoxylem. The number of radiating arms of xylem varies from two to many, the terms **diarch**, **triarch**, **tetrarch**, etc., being used to designate the number of such arms (Fig. 47, I). It should be observed that in this type of stele there is no pith at all, although a stage of development of the stele may be found in which the central metaxylem cells have not yet been differentiated and may, therefore, appear like fundamental tissue.

The radial stele is regarded as the most primitive type of stele. It is found in the roots of all vascular plants but in no stems except those of a few primitive vascular plants like *Lycopodium*.

The Protoste. The protoste (Figs. 82, B; 83, B) is similar to the radial stele in having a solid central core of xylem, but it differs in that this core is cylindrical, not radiating, and is completely surrounded by a cylinder of phloem. There is, again, no pith. By some authors the radial stele is considered a form of protoste. The protoste is found only in the stems of certain genera of primitive ferns.

The Siphonostele. The essential feature of the siphonostele is the arrangement of the vascular tissues in the form of a hollow cylinder with a distinct pith in the center; i.e., the pith occupies the so-called "hollow" portion. The phloem and xylem form concentric cylinders. In the **ectophloic siphonostele** (Figs. 82, C; 83, C) the xylem cylinder lies next to the pith and is surrounded by the phloem cylinder. In the **amphiphloic siphonostele** (Figs. 82, D; 83, D) there are two cylinders of phloem, one lying next to the pith and surrounded by the xylem cylinder, and the other external to the xylem cylinder. The ectophloic siphonostele is the characteristic stele of the dicotyledons and gymnosperms. The amphiphloic siphonostele is found chiefly in certain ferns (*Adiantum*, *Dicksonia*, and *Marsilea*) and in such dicotyledons as members of the cucumber family. The amphiphloic siphonostele is considered the more primitive of the two.

The siphonostele is often considerably broken up by the passage of the vascular elements from the stem to the leaf. Vascular strands passing into the leaf are termed **leaf traces**. When the leaf traces leave the siphonostele, they cause definite breaks, called **leaf gaps**, in the side of the cylinder from which they emerge. Naturally the leaf gaps occur above the leaf traces.

The presence of the leaf traces and the leaf gaps changes the general topography of

the stem in which they occur. A transverse section of a siphonostelic fern stem, for example, cut through an internode at a place not having a leaf gap, shows the vascular tissue as a complete ring, but a transverse section taken through the region of the node shows two crescent-shaped areas of vascular tissue of unequal size, the larger of which is the broken vascular cylinder, and the smaller the leaf trace. The break in the cylinder is always on the side toward the leaf trace and is the leaf gap. The develop-

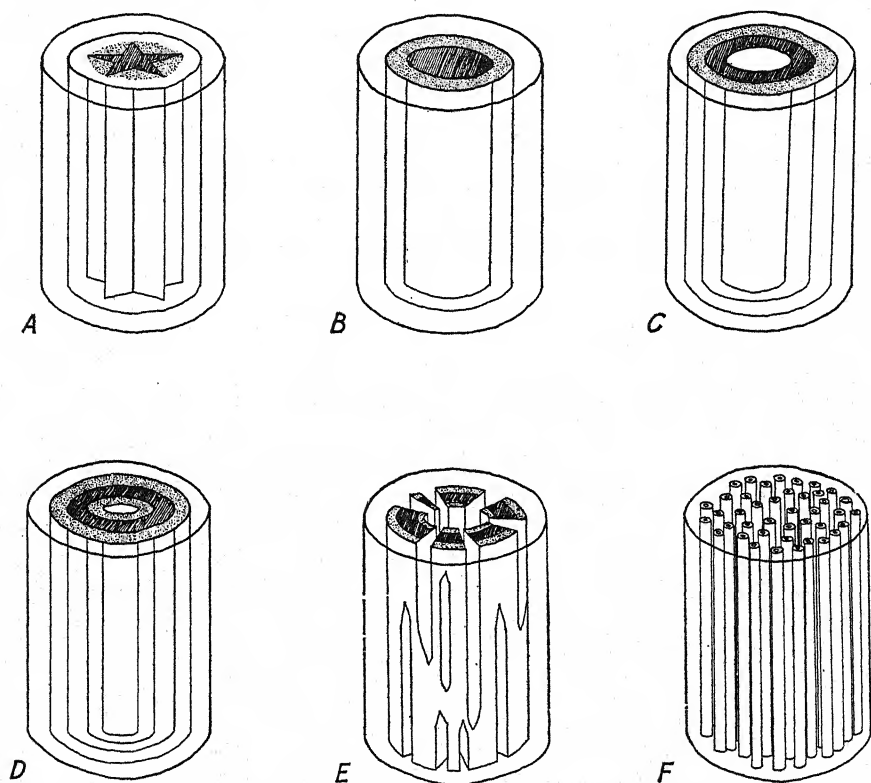
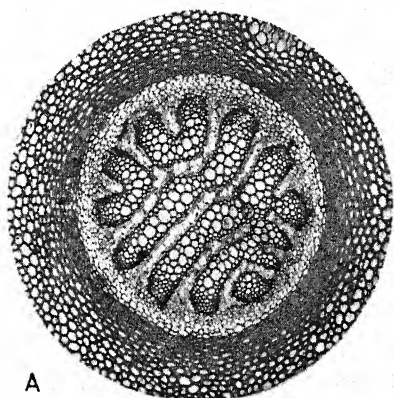


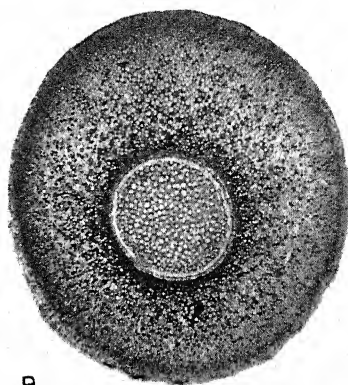
FIG. 82. Diagrammatic representation of types of steles. *A*, radial stele; *B*, protosteles; *C*, ectophloic siphonostele; *D*, amphiphloic siphonostele; *E*, dictyostele; phloem stippled and xylem shaded in each case; *F*, dictyostele of monocotyledons showing scattered, amphivasal bundles. (Drawn by Chris. Hildebrandt.)

ment of the break in the cylinder caused by the leaf trace is but a local condition above which the cylinder resumes its regular cylindrical arrangement.

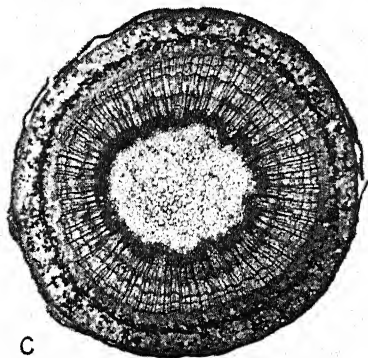
The Dictyostele. In the dictyostele (Figs. 82, *E*, *F*; 83, *E*, *F*) the leaf gaps are so numerous and cause so many interruptions in the vascular cylinder that the whole stele appears to be broken up into distinct strands. The dictyostele is thus merely a greatly dissected siphonostele and actually originates as a siphonostele. The term "dictyostele" means netted stele and is so named because the vascular strands form an anastomosing, or netted, system. These vascular strands should be regarded as distinct pieces of an original siphonostele, the isolation of which has been accomplished by the development of numerous leaf gaps. Such a stele is found typically in certain



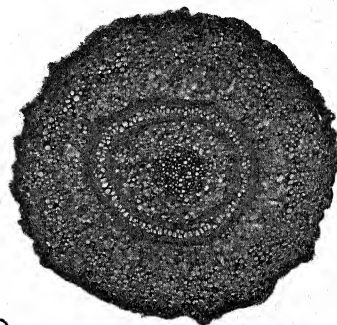
A

Radial stele (*Lycopodium*)

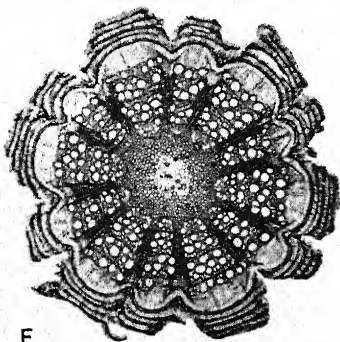
B

Protostele (*Gleichenia*)

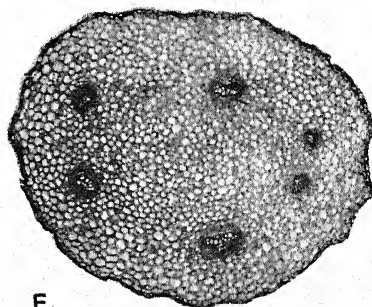
C

Ectophloic siphonostele (*Magnolia*)

D

Amphiphloic siphonostele (*Dicksonia*)

E

Dictyostele (*Clematis*)

F

Dictyostele (*Polypodium*)

FIG. 83. Types of steles as seen in photomicrographs of transverse sections of stems. Compare with Fig. 82. (Photomicrographs by D. A. Kribs.)

ferns and in a number of dicotyledons. The stele of the monocotyledons, with its scattered bundles, is considered to have a similar origin and, although appearing quite different from the dictyostele of other plants, is none the less usually considered a dictyostele.

TYPES OF VASCULAR BUNDLES

On the basis of the orientation of the xylem and phloem, the individual vascular bundles of the stele are classified as **radial**, **concentric**, **collateral**, and **bicollateral**. On the basis of whether or not the bundles contain cambium, they may be classified as **open** (with cambium) or **closed** (without cambium). Some of these types of bundles have already been mentioned in the previous pages.

The Radial Arrangement of Xylem and Phloem. In the early condition of a radial stele, individual groups of xylem cells and of phloem cells are found next to the pericycle, the xylem and phloem lying on different radii and often separated by undifferentiated parenchyma. In this case there are no separate bundles consisting of xylem and phloem but these tissues are said to have a radial arrangement (Fig. 84, A).

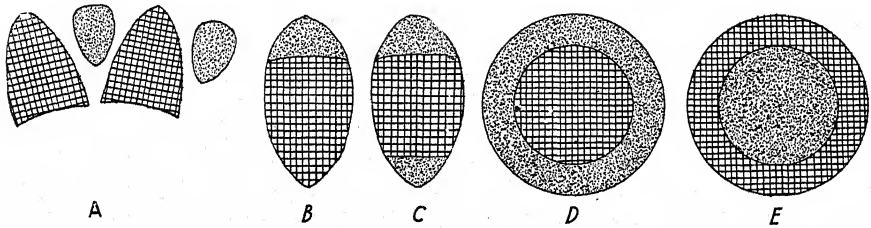


FIG. 84. Diagrammatic representation of types of vascular bundles. A, radial arrangement of xylem and phloem; B, collateral bundle; C, bicollateral bundle; D and E, concentric bundles; D, amphicribal; E, amphivasal; phloem stippled, xylem cross-hatched throughout. (Drawn by F. Brown.)

Concentric Bundles. In the concentric bundle, the xylem and phloem are arranged concentrically; *i.e.*, one surrounds the other, the two forming concentric cylinders. There are two kinds of concentric bundles, the **amphicribal** and the **amphivasal**. In the amphicribal type (Fig. 84, D) the xylem forms a central core and is surrounded by a cylinder of phloem. This type of bundle occurs in some of the ferns. In the amphivasal type (Fig. 84, E) the phloem forms the central core and is surrounded by a cylinder of xylem. Amphivasal bundles are commonly found in monocotyledons with underground stems, like *Acorus*, and often at the nodes of other monocotyledons. Concentric bundles, as a rule, have no cambium and hence are closed bundles.

The Collateral Bundle. The collateral bundle (Fig. 84, B), in contrast to the concentric bundle, is a wedge-shaped strand of vascular tissue in which the xylem and phloem occur on the same radius, with the phloem toward the periphery of the stem and the xylem toward the center. Collateral bundles are characteristic of the stems of dicotyledons and gymnosperms but are also found in some ferns and in monocotyledons like corn and other cereals. In the gymnosperms and dicotyledons, these bundles are of the open type, possessing cambium. In monocotyledons, cambium is absent from the bundle and in addition there is frequently a sclerenchyma sheath around each bundle.

The Bicollateral Bundle. The bicollateral bundle (Fig. 84, C) has the same general features as the collateral bundle but there is phloem both inside and outside the

xylem. The inner mass of phloem, frequently of very limited extent, is located next to the pith. The cambium layer occurs only between the xylem and the outer mass of phloem. All tissues lie on the same radius. Bicollateral bundles are found in stems having amphiphloic siphonosteles, *viz.*, certain ferns and members of the cucumber family. The potato and the tomato have bicollateral bundles in which the internal phloem occurs in small scattered strands.

Open and Closed Bundles. The term **closed bundle** refers primarily to a vascular strand entirely lacking in cambium tissue, so that, after its cells have taken on their mature characteristics, no additional new cells can be formed, and, therefore, no growth of the bundle is possible. Often such bundles also have a definite external bundle sheath of heavy-walled sclerenchyma cells, as in the corn bundle. In addition to these two usual characteristics, all closed bundles originate as strands of meristematic tissue and, therefore, are to be classed as primary tissues. The radial and concentric vascular strands of ferns and the amphivasal and collateral bundles of the monocotyledons are closed bundles.

On the other hand, **open bundles** are characterized by the presence of cambium tissue which enables the bundles to maintain a continuous growth by means of which they increase indefinitely in size. Such bundles also lack a bundle sheath. While many of these bundles originate from strands of meristematic cells, others arise from the activity of cambium tissue at a later period. The collateral bundles of gymnosperms and dicotyledons and the bicollateral bundles of other dicotyledons are all open bundles.

SUMMARY OF THE DISTINGUISHING ANATOMICAL FEATURES OF DICOTYLEDONS, GYMNOSPERMS, AND MONOCOTYLEDONS

Dicotyledons.

1. Primary permanent tissues derived directly from apical meristems and consisting of epidermis, cortex, sometimes an endodermis, pericycle, vascular bundles (consisting of phloem, cambium, and xylem), pith, and pith rays.
2. Presence of cambiums giving rise to strong development of secondary tissues (vascular tissues and periderm).
3. Xylem composed of vessels, tracheids, wood fibers, xylem parenchyma, and wood rays.
4. Phloem composed of sieve tubes, companion cells, phloem parenchyma, and phloem fibers.
5. Concentric arrangement of the tissues, the vascular bundles forming a hollow cylinder.
6. Bundles of the collateral or bicollateral type.
7. Stele—ectophloic siphonostele; in some, amphiphloic siphonostele or dictyostele.
8. In woody stems—definite zones of bark and wood, the wood divided into concentric annual rings.

Gymnosperms.

1. Primary permanent tissues and secondary tissues developed the same as in dicotyledons.
2. Xylem composed almost exclusively of tracheids with bordered pits and wood rays. Complete absence of vessels and wood fibers. Presence of resin ducts in many species.
3. Phloem consisting of sieve tubes and phloem parenchyma—complete absence of companion cells.

4. Arrangement of tissues and bundles as in dicotyledons.
5. Bundles of the collateral type.
6. Stele—an ectophloic siphonostele.
7. Bark and wood and annual rings as in dicotyledons.

Monocotyledons.

1. Primary permanent tissues derived from apical meristems as well as from intercalary meristems. Primary tissues consisting of a base of fundamental tissue through which vascular bundles are scattered.
2. Complete absence of cambium except in a few species and hence no secondary tissues.
3. Xylem and phloem composed of the same elements as in dicotyledons with different proportions of the different elements.
4. Scattered arrangement of vascular bundles, but in a few species the bundles form a hollow cylinder as in dicotyledons.
5. Bundles of the collateral type or amphivasal type, but always closed bundles, often surrounded by a sclerenchyma sheath.
6. Stele, usually considered a dictyostele.
7. Stems not differentiated into bark and wood and no annual rings. Frequently a layer of sclerenchyma immediately inside the epidermis.

FUNCTIONS OF STEMS

General. The most important functions of the stem are probably mechanical support of the leaves, flowers, and fruits and the conduction of water, inorganic salts, and elaborated foods. It is chiefly through the growth and development of the stem that the leaves are brought into proper positions with respect to light while at the same time maintaining their connection with the water and mineral supply of the soil. Thus the leaves are enabled to carry on food synthesis. After the foods are made, the stem again provides the pathway through which these foods are removed from the leaves and carried to other regions of the plant. Similarly, the stem supports the flowers, fruits, and seeds and provides the conducting channels through which these organs are supplied with necessary foods for development. In addition to this, stems usually serve as food-storage organs in the plant. Carbohydrates and other foods may be stored in the pith, the cortex, the phloem parenchyma, and the wood rays. Food storage is a prominent function of the stems of many perennial plants, furnishing for these plants the means of renewing growth in the spring. The stems of some species of plants are also used for water storage. This is true of many of the cacti. Young stems and especially those of herbaceous plants are green and carry on photosynthesis. Finally, the stem sometimes serves as a means of propagating the plant. While the number of species in which this occurs in nature is limited, it is made use of extensively in the commercial propagation of many fruits and greenhouse plants. Such plants as chrysanthemums, coleus, carnations, and roses are

regularly grown from stem cuttings. Fruit trees are propagated by budding or grafting, both of which are types of stem propagation. The advantage to the grower of such asexual methods of propagation is that the new plants come true to the original type, whereas plants grown from seed often do not.

Tissues Concerned in Water Conduction. It has already been mentioned that the xylem, or wood, is the water-conducting tissue of the plant. While, in many parts of the plant, water and dissolved inorganic substances pass through parenchyma cells, it is chiefly through the tracheids and vessels that these substances are transported. The very structure of these elements indicates this, but it can also be demonstrated experimentally. If, for example, a cut stem is placed in a solution of thionin or any other non-poisonous dye and allowed to stand for an hour or more, cut sections of the stem will reveal that only the tracheids and vessels are stained by the dye, proving that the liquid must have passed through these cells. That it did not move primarily in the walls of these cells can be proved by dipping the cut end of a leafy stem into gelatin, made liquid by warming it, and allowing the gelatin to be absorbed by the cut stem. If the gelatin in the stem is allowed to solidify by cooling in water, and a small piece of the end of the stem is then cut off so as to expose the cell walls, and the stem is again placed in water, the shoot will be found to wilt. This wilting results because the cavities of the tracheids and vessels have been clogged with gelatin. Similarly, a leafy shoot that has been allowed to wilt will often fail to recover from the wilted condition when the stem is placed in water because the cavities of the cells are clogged with air. Still further evidence of the path of movement is furnished by girdling. Removing a ring of bark down to the cambium does not cause a plant to wilt, but if the stem is supported and the xylem carefully cut out through a complete section of the stem, without injuring the phloem and cortex, the plant will wilt. This proves that the xylem is the only tissue that can conduct water at a rate fast enough to prevent wilting. In some trees, only the sapwood functions in water conduction, the older wood becoming clogged with tyloses, which are bladder-like protrusions into the tracheids and vessels from the adjacent living parenchyma cells. In other trees the entire xylem continues to function in water conduction. It is generally believed that most of the inorganic substances are also carried in the tracheids and vessels.

Root Pressure. If the entire top of a growing plant is cut off a few inches above the ground and a glass tube attached to the cut end by means of rubber tubing, it will be found that sap gradually rises in the tube. If a manometer is attached to the cut surface, the actual pressure of the sap can be measured. In this case, it will be found that this pressure rarely exceeds 2 atm. and is often lower. The force causing the exudation of the

sap from the cut stem is called **root pressure** because it is thought to be caused by osmotic forces operating in the root. Sap also sometimes flows freely from twigs broken from plants in spring. Such exudation is particularly pronounced in pruned grape vines and other plants. It is sometimes called "bleeding." It is the same force that causes the sap of maple trees to flow in spring when they are tapped for maple-sugar making. Other trees exhibit the same phenomenon.

While the pressure of the sap flow is relatively low, large volumes of liquid are sometimes exuded. A sugar maple may yield 5 to 8 liters per day, a birch 5 liters, and some palms 10 to 15 liters per day. As much as 50 liters per day has been recorded for certain species of palms. The exudate consists of small amounts of sugars and other organic and inorganic substances besides water.

Among the conditions necessary for exudation may be mentioned an abundant supply of water, a favorable temperature, the presence of living cells in the roots, and, in general, conditions that would check transpiration. There is little exudation at very low temperatures. If the roots are killed, no exudation takes place. Exudation is greater at night than it is during the day in leafy plants and in woody plants is far more pronounced in early spring before the leaves come out than during any other season.

The fact that the exudate of many plants contains sugar makes the phenomenon of some commercial importance in the maple-sugar industry and in the making of the Mexican fermented liquor pulque and the distilled liquor mescal. Both of the latter are made from the exuded sap of the century plant (*Agave americana*). In the plant, root pressure may help to lift the sap in low-growing herbs, but it plays very little part in the ascent of sap in tall trees, as will be seen presently.

The Ascent of Sap in Stems. In a previous chapter it was stated that an apple tree may lose as much as 96 gal. of water per day through transpiration. This means that there must be in the stem some method of transporting large quantities of water to the leaves to replace this loss. The question as to how such trees as the giant redwoods of California or the eucalyptus of Australia, species that may attain a height of 300 to 400 ft., can lift the enormous quantities of water required by the leaves, at a rate fast enough to prevent wilting, has interested students of botany for many years. It is not the object of this discussion to present in detail all of the many theories that have been advanced to explain this phenomenon but to review some of the forces that may operate and to explain briefly the most likely method by which the sap rises to the tops of the tallest trees.

Exudation Pressure or Root Pressure. From the fact that a stem may continue to give off water when the entire top is cut off, as mentioned in the preceding section, it might be thought that the sap is forced up from

below by the osmotic forces operating to produce root pressure. Careful consideration of the matter, however, will show that root pressure is a wholly inadequate force in lifting sap to the tops of tall trees. In the first place, such pressure rarely exceeds 2 to 6 atm., whereas it has been estimated that about 20 atm. are necessary to lift the sap to the tops of the tallest trees. Furthermore, root pressure is lowest when transpiration is highest. In addition, it might be mentioned that negative pressures have frequently been registered in the stems of trees. Such negative pressures would not be found if the sap were forced up from below. That the roots are not necessary for the ascent of sap is indicated by the fact that the severed top of the plant does not wilt when placed in water. Not only is this true but accurate measurements show that it will lift the water with a force of several atmospheres. Many plant physiologists believe that root pressure is not even an aid to the ascent of sap.

Atmospheric Pressure. If the outside of the stem were entirely sealed off from air, so that the xylem could act as a straight system of tubes from root to leaf, loss of water at the top of the column might be thought to create a vacuum, with the result that atmospheric pressure, acting on the lower end of the column, might force the water up to prevent the vacuum from being formed at the top. Unfortunately, few of these conditions operate in the plant. There is no free surface at the bottom of the column upon which atmospheric pressure could operate, since the water is lifted from living cells of the roots. Furthermore, the maximum height to which atmospheric pressure could lift the sap, even if all the necessary conditions were operating, would be less than 32 to 33 ft.

Capillarity. The fact that vessels and tracheids, through which the sap rises, are capillary tubes suggests immediately that some liquid could rise in these elements by capillarity. Undoubtedly, capillarity does operate in the wood, but from the known diameters of the vessels and tracheids it is obvious that such rise could not exceed a few feet at the most. It is a well-known fact that the smaller the capillary tube the higher will a liquid rise in it. We should, therefore, expect to find that the tallest trees would have the smallest vessels, but the reverse is often actually found to be true. Furthermore, in many trees the spring wood, which is developed when the need for water is greatest, is usually made up of larger vessels than is the late summer wood. For these as well as other reasons, capillarity may be dismissed as a force taking any active part in sap ascent.

Other Possible Forces. One of the older theories regarding sap ascent assumes that the water is vaporized at the bottom of the column and passes up as vapor to the top of the column where it is condensed back to a liquid. In addition to the difficulties involved in considering the effect of temperature on such vaporization and condensation, even if it did take place, such a

method could not operate with sufficient speed to supply the demands of the plant during rapid transpiration and would account for the movement of pure water only and not the movement of inorganic substances dissolved in the sap of the vessels and tracheids.

The great German plant physiologist Julius Sachs believed that the water moved in the walls of the xylem cells by imbibitional force. Water is undoubtedly found in the walls of the xylem cells; but from the fact that plants wilt when the cavities of the vessels are clogged, it is obvious that this method could not supply the water fast enough.

The late plant physiologist Bose, of India, revived another of the older theories, *viz.*, that the living cells all along the stem and, according to Bose, particularly those of the inner cortex provide osmotic forces which force the sap upward by a sort of system of relay pumps. This theory has little support anatomically or experimentally. It has been found that the sap still continues to rise after all the cells have been killed in long sections of the stem extending over many feet.

The Cohesion Theory. Up to the present time the most satisfactory explanation that has been offered to explain the ascent of sap is the cohesion theory. This theory assumes that the water is drawn up through the xylem by a pull applied at the top of the water column and that this pull is transmitted downward through the **cohering water** in the vessels and tracheids. The pull, at least during high transpiration, is caused by the evaporating power of water in the leaves but is limited in amount by the osmotic pressure of the leaf cells. The pull may also be created by a water deficit in the hydrophilic colloids of the cells at the top of the water column. This deficit tends to be relieved by creating a pull on the water in the vessels and tracheids. The water column in these vessels and tracheids does not break because of the tensile strength (cohesion) of the water column itself. It has been estimated that the total pull required to maintain the column at maximum transpiration does not exceed 20 atm. The osmotic pressure of the leaf cells has been found to average around 30 atm. and hence is adequate to create this pull. Furthermore, the imbibitional force of the colloids of the leaf and of the young twigs may reach a value of several hundred atmospheres. The tensile strength of the sap has been measured and found to exceed 150 atm. in some cases. This force also seems to be more than adequate. The theory assumes that there is an unbroken water column from roots to leaves. This apparently has also been found to be true, although many of the cells of the xylem may be filled with air without destroying the continuity of water. It might further be mentioned that the fact that negative pressures of 10 to 20 atm. have been observed in stems supports a theory which assumes that the sap is pulled up from above rather than forced up from below. Furthermore, the tracheae,

which are exclusively water-conducting cells, are usually thickened by rings, spirals, and bars on the inside, which enables them to withstand a pull from the top of the column rather than a pressure from below or within the cells.

The cohesion theory explains the ascent of sap exclusively on a physical basis. It excludes the living cells along the water column from taking any part in the lifting of the sap, although it requires the cells at the top of the column to be living cells. It should also be remembered that the water reaches the xylem at the bottom of the column through the living cells of the root, even though these cells may take no part in actually causing the sap to rise. Consequently sap ascent takes place only in a living plant.

At the present time there is more experimental evidence in support of the cohesion theory than of any other theory that attempts to explain the ascent of sap.

Conduction of Food. The xylem is concerned chiefly with the conduction of water and inorganic substances. Since there are many storage cells in the wood rays lying next to the xylem vessels and tracheids, it is not unusual to find such foods as sugars in the sap of the xylem. It is generally believed, however, that the principal channel for the translocation of elaborated foods is the phloem. The structure of the sieve tubes is such as immediately to suggest conduction as their main function. Furthermore, chemical analysis of the contents of the phloem cells shows them to consist largely of dissolved carbohydrates, proteins, and other nitrogen compounds. It is often found that sieve tubes are largest and the phloem better developed in stems in which there is obviously a rapid and large movement of food, as in the peduncles of some flowers and large fruits and in many of the elongated stems of cucurbits such as the pumpkin and the squash. That the phloem is the chief food-conducting tissue is also proved by girdling experiments. If a ring of bark is removed from the lower part of a cutting of willow or privet and the cutting placed in water, roots will develop only above the girdle, showing that the food necessary for their development can be obtained only from the upper part of the stem. If the xylem carried the food, roots should develop below the girdle as well as above it. The fact that girdling of apple trees in early June sometimes increases the production of blossoms and fruit the following year also indirectly supports the contention that the phloem carries the food, since it is thought that the development of flower buds is conditioned by the carbohydrate supply in the stems at this time. When stems are left intact, much of the carbohydrate moves to the roots. Girdling prevents the movement to the roots and thus tends to increase the carbohydrate content of the stem above the girdle. If the girdling is done at any other season of the year than spring, it often kills the plant through starvation of the roots, a fact which again indicates that the phloem carries the food.

While there is considerable evidence that foods are transported in the phloem, little is accurately known concerning the mechanism of this movement or the forces that bring it about. There is some evidence that some of the inorganic salts may also be transported in the phloem. Apparently these minerals as well as the foods can move upward as well as downward in the phloem.

STEMS OF UNUSUAL FORM AND FUNCTION

Stems, like leaves and roots, may have forms and perform functions not associated with those of the typical organ or at least not associated with the majority of stems. Deviations from the types of stems thus far described are widespread and numerous. Some of the more prominent, important, and unusual ones are described in this section.

Underground Stems. All underground, or subterranean, stems may be looked upon as unusual, since one of the primary functions of the ordinary stem is that of displaying leaves to the light. Because of their underground position they are often mistaken for roots. There are four principal kinds of underground stems, *viz.* **rhizomes, or rootstocks, tubers, corms, and bulbs.**

Rhizomes, or Rootstocks. The rhizome, or rootstock, in the least modified form is merely a horizontal stem growing beneath the surface of the soil. In some cases, it is only partly covered. It may be compared with the prostrate or creeping aerial stem. Though often erroneously called roots, rhizomes are really stems, as is evident from the fact that they consist of a series of joints which are the stem nodes. At each joint or node there is a leaf, commonly reduced to the form of a small scale. In the axil of this leaf a bud is produced. Thus rhizomes, like typical stems, are characterized by the presence of nodes and internodes, leaves, and axillary buds. Roots have none of these features. Rhizomes give rise, at the nodes, to roots as well as to leaves and buds. This is also true of many horizontal aerial stems and of the upright stems of certain plants if they are placed in a moist environment. Such roots are easily distinguished from the stems which give rise to them.

Plants with rapidly elongating rhizomes, such as Canada thistle and quack grass (Fig. 85), spread quickly and widely. When cut up, as in plowing and cultivating, each piece produces a new plant. It is this feature which makes such plants obnoxious weeds, difficult to eradicate. Rhizomes are perennial structures that live over the winter. In the spring some of their buds develop into upright leafy shoots which eventually produce flowers and seeds, while others form new subterranean shoots. This is repeated again and again. In the meantime, the older portions of the rhizomes often die, thus severing the connections between younger branches and giving rise to many separate plants. A rhizome may be cut

into as many pieces as there are nodes and each piece will produce a new plant if there is sufficient food stored in it to enable the bud to develop into an aerial shoot. Furthermore, pulling or cutting off the top of a plant with rhizomes does not kill it. New shoots are readily produced from the underground buds. This situation is very different from that of the ordinary plant with only roots as subterranean parts. Cutting off the top of the ordinary plant completely destroys it except in unusual cases in which the root is capable of giving rise to adventitious buds. Repeatedly cutting

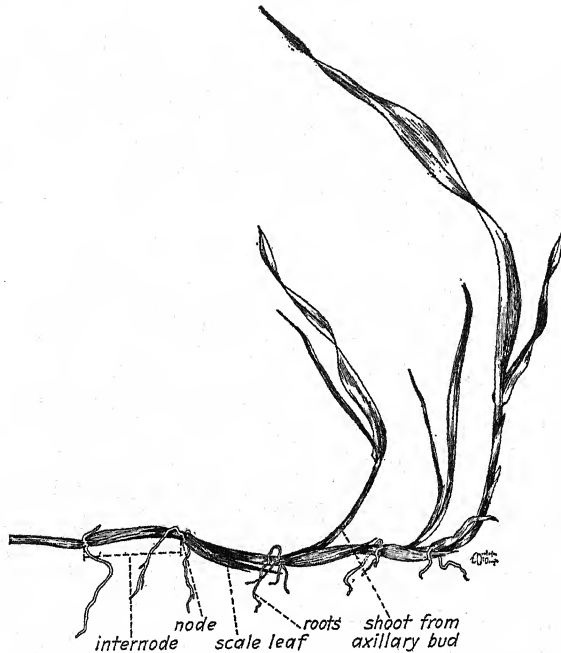


FIG. 85. Quack grass (*Agropyron repens*), showing underground stem or rhizome, bearing roots, leaves, and aerial shoots. (Drawn by Elsie M. McDougle.)

off the shoots as they develop from a rhizome will, however, ultimately cause the stored food reserves to be exhausted and will kill the plant.

In some plants the rhizome elongates less rapidly, becomes short and stout, and contains a considerable amount of stored food, usually starch. The length of the living portion of such rootstocks varies from less than an inch to a foot or more. Iris, canna (Fig. 86, *A*), some mints, and Solomon's seal (Fig. 86, *B*) furnish examples of this type. Many common forms of iris have rootstocks which are partly uncovered and bear true leaves which closely overlap each other because of the shortened internodes. Leaf scars in the form of rings mark the former points of attachment of the leaves. In the mints the rootstock is buried and only scale leaves are formed.

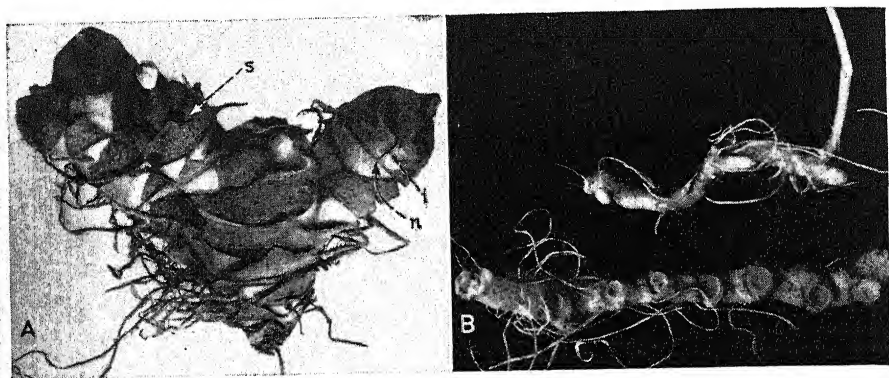


FIG. 86. *A*, rhizome of canna, showing scale leaves, *s*, nodes, *n*, and internodes, *i*; *B*, rhizomes of Solomon's seal, showing circular scars (seals) left by abscised stems, nodes, and internodes.

In Solomon's seal the rootstock is also buried. Each year it sends up at the end of the rootstock a single shoot which bears the foliage and flowers and dies in the autumn, finally separating from the rootstock. A circular

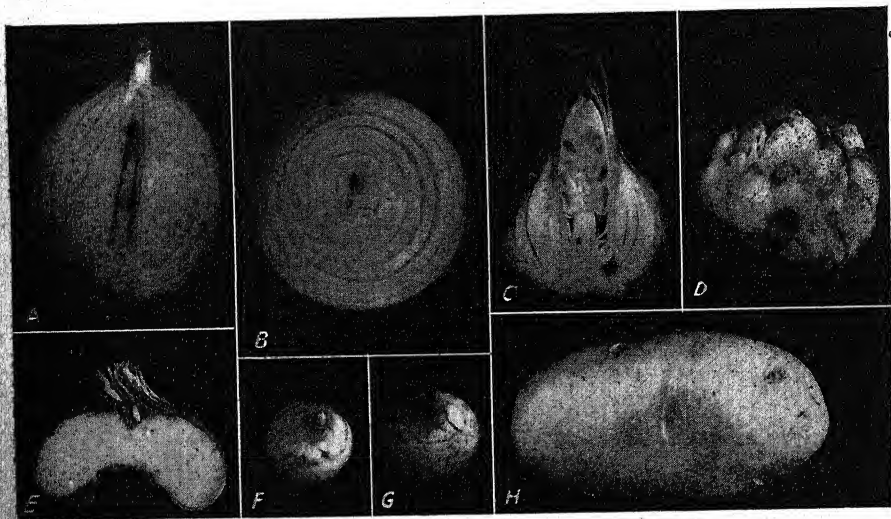


FIG. 87. Modified stems. *A* and *B*, tunicate bulb of onion in vertical and transverse sections, showing scales, which are leaf bases, and a very short stem; *C*, tunicate bulb of *Hyacinth*, showing a partially differentiated flower cluster within the bulb; *D*, scaly bulb of Easter lily; *E-G*, corms; *E*, *Gladiolus*; *F* and *G*, *Crocus*; the rings shown on *F* and *G* are nodes; *H*, potato tuber; the eyes are nodes with buds.

scar is left at the point where the shoot was attached. Because this scar looks something like the impression of a seal upon wax the plant came to be called Solomon's seal. Since but one "seal" is formed each year, the limits of the years' growth of the rootstock can easily be determined.



FIG. 88. Modified stems. *A*, Boston ivy (*Ampelopsis tricuspidata*), showing branched tendrils with adhesive disks at their tips; *B*, grape tendrils (*Vitis* sp.); *C*, butcher's-broom (*Ruscus* sp.); the leaflike organs are modified stems (cladophylls), at the center of each of which is a node with a scale leaf and an axillary bud producing flowers; *D*, thorns of buckthorn (*Discaria* sp.) which are branches arising from buds in the axils of leaves and themselves bear leaves at the nodes.

Tubers. When rhizomes become enlarged at the growing tips by the accumulation of stored food, commonly starch, tubers are produced, like those of the Jerusalem artichoke or the potato (Fig. 87, *H*). The "eyes" of the potato are nodes at each of which several buds are produced in the axils of small scale-like leaves. Tubers are organs of food storage. In the autumn the rootstock dies except for the tubers which are left disconnected in the ground, each one capable of producing new plants in the spring. Potatoes are regularly propagated by cuttings of the tubers.

Corms, or Solid Bulbs. A corm, illustrated by the crocus (Fig. 87, *F-G*), is a very short, thick rhizome, or rootstock, often much broader than long

and usually growing upright rather than horizontally. Buds and roots are often produced at the nodes. The buds produce the new plants. Some of them, after a time, grow into new corms and the old one dies. The scaly husk of the corm consists of the dead remains of leaf bases. These are quite prominent on gladiolus corms (Fig. 87, *E*).

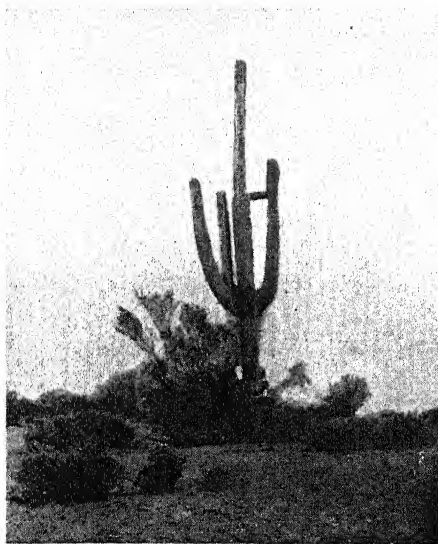


Fig. 89. The giant cactus (*Saguaro* sp.) (Photograph by Dr. F. W. Owens.)

Bulbs. The bulb may be regarded as a short stem with fleshy leaf bases, commonly called scales. When the scales extend completely around the bulb, so as to appear in cross section as a closely compacted series of concentric rings, as in the onion (Fig. 87, *A, B*), the bulb is said

to be *tunicate*, or *coated*. The tulip, hyacinth (Fig. 87, *C*), and leek are also of this type. When there are numerous narrow scales, not completely encircling the stem, as in the lily, the bulb is said to be *scaly* (Fig. 87, *D*).

Aerial Stems of Unusual Form. Aerial stems may be unusually long, as in plants with climbing or creeping stems. *Climbing stems*, or *vines*, usually rest upon or are attached to some support and often climb by means of special devices. Those of the *rambler* type simply rest on the tops of other plants, often on bushes and rapidly growing herbs. Many of these stems have epidermal outgrowths in the form of prickles or spines which enable them to stick to their support. Certain roses, briars, and bitter-sweet are ramblers. *Root climbers*, such as climbing hydrangea (Fig. 49),

English ivy, and poison ivy, climb by means of adventitious roots arising along the side of the stem in contact with its support. *Tendrils* climb by means of tendrils, which are sometimes modified leaves or leaf parts, as described under the section on unusual leaves. In some cases, however, the tendrils themselves may be modified stems as in the grape and Boston ivy (Fig. 88, A, B). The tendrils of the Boston ivy are provided with adhesive disks. In the case of *twiners*, the entire stem winds about its support. Examples may be found in the morning-glory, pole beans, and false bittersweet.

Creeping, or prostrate, stems trail along the surface of the ground and take root at the nodes. Trailing arbutus, ground pine, and partridge berry have such stems. Those of the strawberry, called *runners*, eventually take root at the tips, form buds, and give rise to new plants. Stems like those of black raspberry, currant, gooseberry, or dewberry bend over to the ground, take root, and send up a vigorous shoot which becomes an independent plant when the parent stem dies or is cut. Stems of this type as well as some creeping stems that regularly root at the nodes are sometimes called *stolons*. *Offsets* are shorter branches, radiating outward along the ground in all directions from a main stem and forming clusters of leaves at their tips. These are formed in old hen-and-chickens, some lilies, and houseleek.

Other types of unusual aerial stems include *unusually short stems* found in the so-called stemless plants, such as the dandelion and the common plantain, and *aerial bulblets*, which are similar to small underground bulbs and which are formed in the axils of tiger-lily leaves and on the flowering shoots of onions. It is obvious that aerial as well as underground stems may be *organs of vegetative propagation*.

Stems in plants having highly modified leaves which carry on little or no photosynthesis or in plants with ephemeral leaves may be the chief photosynthetic organs of the plant. In some cases represented by such plants as asparagus and butcher's-broom (Fig. 88, C), these stems simulate leaves and hence are called *cladophylls*. Sometimes they are stout and fleshy as in cacti (Fig. 89) and many other xerophytes. These stout, fleshy stems are also frequently storage organs for food and water.

Finally, stems, as well as leaves, may be thorn-like. *Thorns* may be unbranched as in the Osage orange and thorn apple or branched as in the honey locust and buckthorn (Fig. 88, D). Honey-locust thorns usually arise from supernumerary buds.

CHAPTER 9

GROWTH AND MOVEMENT

INTRODUCTION

An exact definition of the term "growth" is scarcely possible. Fundamentally, it is one of the attributes of living protoplasm. It is the sum of those activities of protoplasm whereby a living organism progresses from a less mature to a more mature condition. It can take place only where there is constructive metabolism, culminating in assimilation, which is the making of living substance out of nonliving. Growth usually involves an increase in mass and volume, *i.e.*, an increase in weight and size; yet mere increase in weight or size is not necessarily growth. A seed, for example, may swell to many times its original size by the mere absorption of water before any growth at all takes place. Or, again, a seed developing on the plant may increase markedly in weight through the deposition of food without manifesting any growth. Growth is more than a mere increase in weight or size. It involves a progressive change in form. This latter feature of growth is sometimes called **development**. It is manifested when an undifferentiated leaf primordium develops into a leaf or when a unicellular fertilized egg develops into a multicellular embryo. In both cases there is active growth. Furthermore, the change in form is irreversible; *i.e.*, the differentiated organ resulting from growth cannot revert back to the undifferentiated form from which it originated. Thus growth may be looked upon as an increase in mass or volume, accompanied by an irreversible change in form and structure, all resulting from the activities of protoplasm. True growth, therefore, is restricted to living organisms.

In the measurement of growth, it is usually increase in weight or size that is measured. Increase in weight and size usually occurs even in such cases as the sprouting of potatoes in cellars or the germination of seeds in the dark. While the whole potato tuber or the whole seed in these instances is losing weight by respiration and transpiration, the actual growing organs are increasing in weight and size at the expense of the stored food reserves. In the growth of green plants in light, the increase in weight and size results from the absorption of materials from the exterior and from the synthesis of new substances within the plant.

The growth of organs of higher plants involves not only the enlargement of cells already present but also the formation of new cells. The formation

of new cells by the division of those already present and their subsequent enlargement and maturation to their permanent forms provide the principal means of growth of any multicellular organ. Indeed, the entire plant body is developed from a single cell, the fertilized egg, which, by repeated division, develops into the mature plant. Because of its importance in growth, cell division is taken up in considerable detail in the pages that follow.

CELL DIVISION

In most plant cells, division may be considered as involving both the nucleus and the remainder of the cell. First, the nucleus divides by a process called mitosis. Generally, but not always, this is accompanied by division of the cytosome and followed by formation of a cell wall separating the two new protoplasts.

The Division of the Nucleus—Mitosis. When the nucleus enters into a period of division, it is possible to recognize chromosomes as distinct entities in contrast with the nuclear network, or reticulum, of the non-dividing nucleus (Figs. 4 and 5). As division proceeds, the nuclear membrane and the nucleoli present in the resting nucleus gradually disappear. Soon the nucleus begins to elongate and the division spindle, or achromatic figure, appears. The typical spindle is drawn to points or poles at its ends and presents a circular view in cross section (Fig. 90). The spindle is important in the dividing nucleus because it is the cellular mechanism for the final separation of the longitudinally divided chromosomes into two equal groups. The term achromatic figure as applied to the spindle in a dividing nucleus refers to its lack of affinity for the nuclear stains used to differentiate the chromatin. In most cases, the spindle is formed from the nuclear gel. The conspicuous radiating masses called asters that are seen at the poles of the division spindle in the cells of most animals and in the reproductive cells of some plants, however, are probably cytoplasmic in origin. The asters consist of a central body, the centrosome, and often an extensive system of radiating strands. The centrosome, or central body, of the aster is a definite cytosomic body that originates or is carried in the cytoplasm. The polar asters of the achromatic figure may therefore be regarded as cytoplasmic structures. When the division is complete, it is evident that some material of the old division spindle is left out of the reorganized nuclei and remains in the cytoplasm (Fig. 91). It is not certain that this is ever again incorporated into an achromatic figure.

Once a nuclear division has been initiated in a cell, it becomes a process of constant change, and the chromosomes, generally clearly discernible, appear to be in continuous movement. Although nuclear division is usually described in terms of discrete phases, these are actually not separated phenomena, but are a part of a continuous process, and each phase merges

into the next. In the order of their sequence, the customary stages recognized in nuclear division are the **prophase**, **metaphase**, **anaphase**, and **telophase**. These terms are used to identify the more conspicuous stages of the dividing nucleus.

The Prophase. In the early stages, or **prophase**, of nuclear division, long, slender threads appear in the nucleus. These are the central threads, or

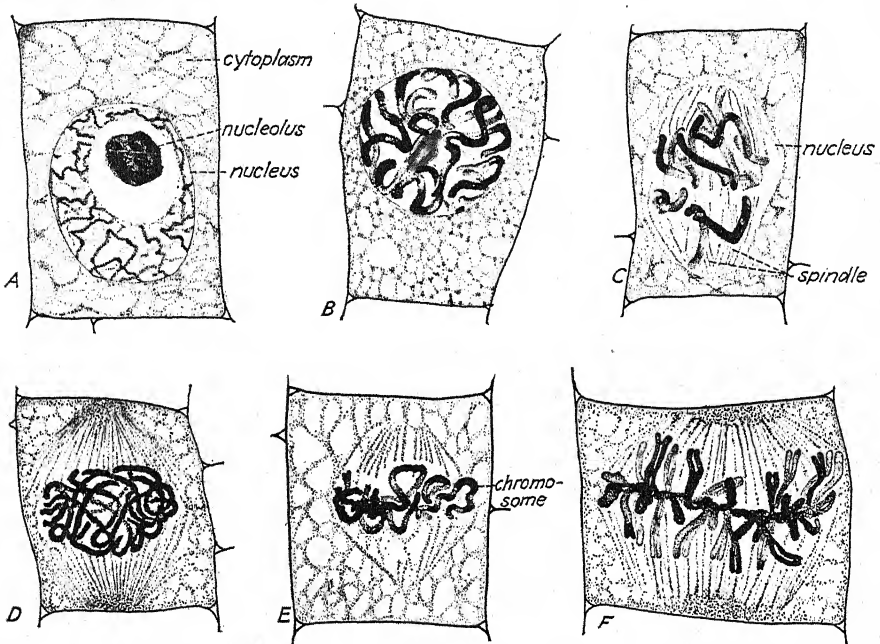


FIG. 90. Mitosis in cells of root tip. A-D, prophase stages; E-F, metaphase stages; A, early prophase; B, medium prophase with chromosomes forming; C, later prophase, nuclear membrane disappearing and spindle forming; D, later prophase, spindle becoming distinct and chromosomes grouping toward equator of spindle, nuclear membrane not evident; E, early metaphase, chromosomes definitely at equator of spindle; splitting of chromosomes can be seen in some instances; F, later metaphase, chromosomes grouped at equator of spindle; each chromosome shows a definite longitudinal split.

chromonemata, of the chromosomes. The term **chromonema** (plural, chromonemata) means literally colored thread and indicates the affinity of these structures for the nuclear dyes. Structurally a chromosome consists of the centrally located, often coiled, chromonema and a surrounding matrix (Fig. 93, A). Chromonemata are thought to be the structures that contain the genes, and their behavior during nuclear divisions is important in the distribution of the hereditary units to the cells. While the chromonema seems to be a permanent feature of the chromosome, the structure and general nature of the matrix seems subject to fluctuation. It appears

to diminish and to lose its affinity for stains at certain periods and by increase in amount and stainability becomes prominent at others.

During the prophase of nuclear division, each of the slender chromonemata appears to be split longitudinally. This splitting is preliminary to the separation of the two halves at a later phase. Although each of the

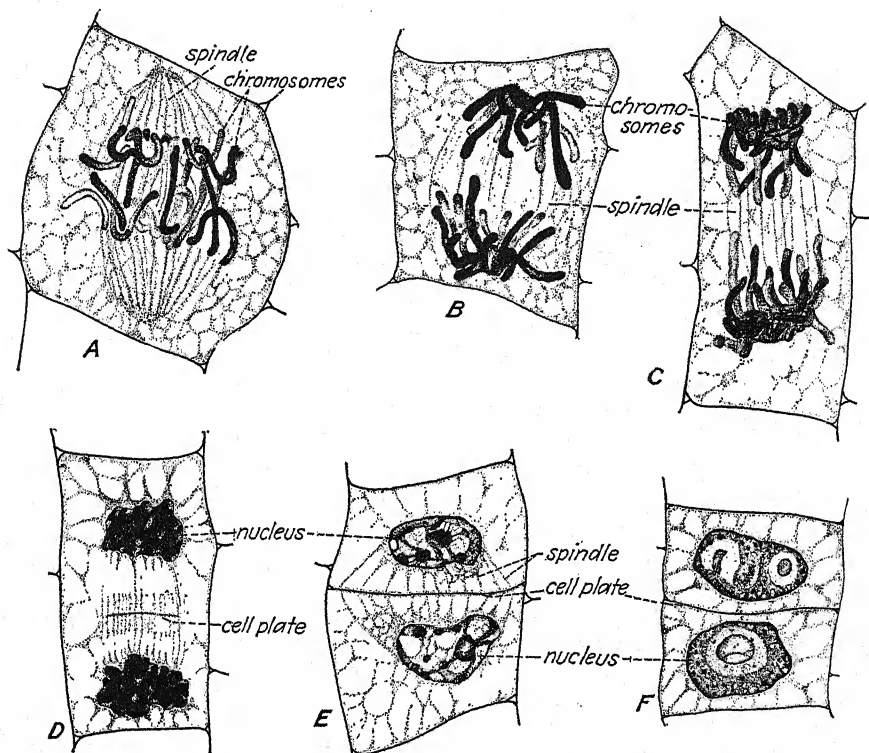


FIG. 91. Mitosis (continued from Fig. 90). *A-B*, anaphase; *C-F*, telophase; *A*, early anaphase; the split halves of the chromosomes are passing from the equator toward the poles of the spindle; *B*, late anaphase; most of the chromosomes have reached the poles of the spindle; *C*, early telophase, chromosomes grouping at each pole of the spindle; *D*, somewhat later telophase, chromosomes rounding up at poles, preceding the formation of nuclear membrane, cell plate forming on spindle at equator; *E*, late telophase, nuclear membrane formed around new nuclei, spindle becoming indistinct; cell division is completed by formation of new wall from the cell plate; *F*, two new cells formed as a result of mitosis.

chromonemata is double as the result of the longitudinal split, this feature is often difficult to demonstrate microscopically. Later in the prophase, coiling of these longitudinally split chromonemata occurs, and they appear shorter and thicker. At about the same time, the matrix can be seen more easily, and presently the structures take on the appearance of typical chromosomes. The matrix of the chromosomes in the later prophase and

following phases develops an affinity for nuclear stains. For this reason, the double nature of the chromosome structure tends to be obscured during a considerable part of the division process. As the division proceeds, these chromosomes, each with its double chromonema, or central thread, move to the middle section of the developing spindle (Fig. 90, *D*). This event marks the approximate end of the prophase, or first stage, of nuclear division.

The Metaphase. During the **metaphase**, or later phase of mitosis, the division spindle is completed and the chromosomes are assembled in a circular plate at its middle, or equatorial, region. In favorable material, the longitudinal split that appears in the chromonemata during the prophase and that has been obscured by the deep staining matrices of the chromosomes again becomes evident at the metaphase. Each of the chromosomes appears to consist of two longitudinal parts, or halves, that now may be called **chromatids**. This term means literally the descendants of a chromosome. The half chromosomes, or chromatids, are thus daughter chromosomes and their individuality will become more pronounced as division proceeds. The arrangement of chromosomes on the spindle is such that one of each pair of chromatids is directed toward one of the poles of the spindle and the sister chromatid toward the opposite pole. When the chromosomes are aggregated at the equator of the spindle, the division has reached the metaphase. In most cases, the metaphase is probably of short duration.

The Anaphase. The chief events of the **anaphase** are the complete separation of the two halves of each chromosome and their movement or migration to one of the two poles of the division spindle. The prefix *ana* in the term anaphase comes from the Greek and means "return," or "going back." Thus the term anaphase means that stage of division during which the chromosomes go back to a nucleus after undergoing longitudinal splitting at the equator of the division spindle. As division proceeds into the anaphase, the chromatids, or daughter chromosomes, separate farther and each moves toward one of the two poles of the division spindle (Fig. 91, *A-C*).

At this stage, the division spindle appears to contain numerous kinds of fibers. Some, called continuous fibers, reach from pole to pole and apparently have no connection with any of the chromosomes. Others, connected with the chromosomes, are called chromosomal, or tractile, fibers. They are attached each to a chromatid and extend toward the poles of the achromatic figure. The point of spindle fiber attachment is designated by various terms, such as insertion region, spindle fiber attachment, kinetochore, centromere, and many others. Although the term centromere means literally central body, the spindle fiber is not always attached

in the middle and only very rarely exactly at the end of a chromatid. The location of attachment of the spindle fiber is definite and constant for each chromosome and may be anywhere between the two ends. The point of spindle fiber attachment divides the chromosome into two parts that are called the arms of the chromosome. As the sister chromatids separate at the equator and move toward the poles of the spindle, generally the part of the chromatid containing the fiber attachment is nearest to the pole, with the arms extending backward toward the equator. If the tractile fiber is attached near the middle region of the chromatid, the structure forms a V shape. In other cases, the migrating chromatid assumes the shape of a hook.

The tractile fibers appear to assist or to guide the chromatids to the poles of the spindle after their separation at the equator. The forces involved in chromosome movement are, however, obscure. Although it appears that the tractile fibers may exert a pulling movement, this has not been demonstrated. Sometimes a third type of fiber may be seen stretching from tip to tip of the separating chromatids. These have been called interzonal fibers.

The Telophase. As the two groups of chromatids reach opposite poles of the division spindle, they each begin to round up into a spherical mass. The chromatids, which may now be called chromosomes, clump together and again become indistinguishable as individual entities (Fig. 91, *D*). Toward the end of the telophase, definite nuclei are reorganized at each of the two poles of the spindle, with one of the clumps of chromatids as the center of each. During the reorganization of the two new nuclei, nuclear membranes are formed and the chromatin net, or reticulum, characteristic of the resting nucleus appears. Meanwhile, the number of nucleoli typical for this plant again become visible. With the reorganization of the two new nuclei, the telophase, or the last stage, of nuclear division is completed.

After the division is completed and the two new daughter nuclei are formed, they may each resume the resting, or metabolic, stage generally known as the interphase. Far from being a period of rest the period of this phase is one of physiological activity. The nucleus may be thought of as passing from one resting stage to another with a period of division between them. Or, again, the nucleus by a process of growth passes from a resting stage into an actively dividing stage by means of which two new nuclei are formed, both of them subsiding again into a resting stage. The duration of the interphase, or stage between divisions, varies. In some cases, when division is rapid, the nuclei scarcely reach a resting stage before the next division begins. In other cases, the nucleus may remain in an interphase for an indefinite length of time.

During the interphase, the material of the chromosomes, the chromatin,

appears to be distributed through the nucleus in the form of a net, or reticulum (Figs. 4 and 5). Because of this condition, individual chromosomes are difficult to recognize. Although they are thought never to lose their identity as structural units, they appear at this stage as a mass of overlapping netted material. Actually the chromosomes in this condition are the exceedingly attenuated chromonemata of the chromosomes which have apparently lost all or most of their surrounding matrices. These threads become dispersed throughout the nucleus, and their overlapping presents the appearance of a network.

The Division of the Cytosome—Cytokinesis. While the division of the nucleus is an important feature of the process, it is not the whole of cell division. In the ordinary vegetative, or somatic, tissues of plants mitotic division of the nucleus is usually accompanied by a division of the cytosome, or cell body. This process, called cytokinesis, generally starts in the telophase of the nuclear division (Fig. 91, *D-E*). During the telophase when the daughter nuclei are forming, the division spindle begins to expand at the equatorial region. This expansion continues until the spindle material together with some cytoplasm makes contact at the side or lateral walls and forms a diaphragm across the mother cell. The term phragmosome, or phragmoplast, which means a barrier or separating body, may be applied to this equatorial structure. In some cases, a cytoplasmic diaphragm may be formed across the cell before the nucleus undergoes mitosis. Visual evidence of cytosomic division is the development of a thin transverse line of material called the **cell plate** at the equator of the division spindle. It is thought that in the early stages of its formation the cell plate consists of fluid material that soon becomes solid. The cell plate increases by accretions, becoming thicker and longer and gradually expanding until it reaches the side walls of the cell. The cell plate represents the early stages in the formation of the middle lamella of the end wall of the new cells. Although cell-plate formation is visual evidence of cytosomic division, cytologists consider that division of the cytosome is actually accomplished when plasma membranes are formed by each of the new protoplasts. The presence of plasma membranes sometimes may be demonstrated before there is much evidence of wall formation. The formation of the cell plate may be regarded as an accompaniment rather than a cause of cytosomic division. The formation of the cell plate and eventually the cell wall between the two plasma membranes is the result of the joint activities of the two new protoplasts. During cytokinesis, the cytoplasmic mass, the plastids, and the mitochondria in the cell are separated and approximately half is incorporated into each of the new cells.

In the cleavage divisions of the embryonic cells of animals and often in the formation of spores in plants, division of the cytosome, following nuclear

division, is accomplished by a process of **furrowing**. In this type of cytokinesis, the separation of the cytoplasm begins at two or more points at the periphery of the cell and proceeds inward toward the center forming a deep cleft or furrow. These furrows eventually meet in the center of the cell, thus cutting the cytosome into two or more parts, the number depending upon the type of nuclear division that is involved.

In summarizing the process of cell division, it may be said that it consists of two fundamental features: nuclear division, or mitosis, and the division of the cytosome, or cytokinesis. During nuclear division, the chromosomes, with their hereditary units, the genes, are each split longitudinally forming two chromatids, or daughter chromosomes. During the splitting process, the genes which are arranged in linear order in the chromonemata of the chromosomes are each divided or duplicated, thus a replica of each gene is present in each of the two chromatids resulting from the longitudinal splitting. In mitosis, longitudinal splitting of the chromosomes is followed by a complete division of the nucleus into two. Each newly formed nucleus thus receives one half of each original chromosome. In this way, the hereditary material is equally distributed to the two new cells without any change in chromosome number. During cytokinesis, the cytoplasm, plastids, mitochondria, and all other cytosomic materials are also divided between the two daughter cells each usually receiving approximately equal portions.

The daughter cells thus formed become entire cells, and the chromatids develop into mature chromosomes like those of the parent cells. Although nuclear division is a continuous process, for the purposes of study it is divided into four phases or recognizable periods. When the division of the nucleus has been followed by the division of the cytoplasm of the mother cell, cell division is fully accomplished. It should be further emphasized that cell division is a fundamental feature of growth.

Duration of Mitosis. Studies have been made of the duration of the mitotic divisions in several types of plant cells. Technical difficulties inherent in the study of dividing nuclei in living cells have limited the number of such studies as well as their results. They show, however, that differences in temperature within the limits of viability are accompanied by differences in the duration of the various mitotic phases. Mitosis in the alga *Spirogyra* has been observed to be accomplished within periods varying from 45 min. to several hours. Observations on stamen hairs of *Tradescantia* (Fig. 92) have shown that the final phases of mitosis from the early anaphase to the completion of cell reorganization occupy periods varying from 45 min. to 2½ hr. From these and other studies, the conclusion may be drawn that the duration of mitosis may be little more than a half hour or may extend over a period of several hours.

Structure and Individuality of the Chromosomes. From the time of the development of the idea that the chromosomes are the bearers of the units of heredity and are therefore the physical basis of heredity, a great amount of study has been devoted to the nature and structure of these cell parts. The most dependable observers report

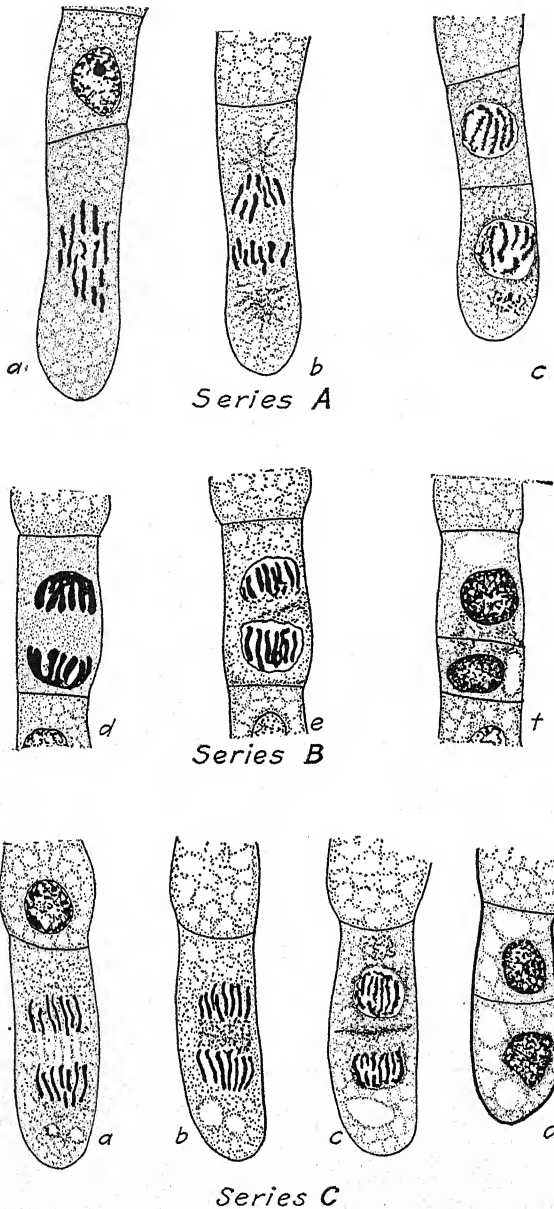


FIG. 92. Duration of nuclear and cell division observed in living cells of young stamen hairs of *Tradescantia*. In each series, the same cell was observed at different times. Series A: *a*, metaphase as it appeared at 4:20 P.M.; *b*, anaphase observed at 4:50 P.M.; *c*, division of cell complete, with the transverse wall formed, observed at 6:50 P.M. Series B: *d*, late anaphase as observed at 4:35 P.M.; *e*, telophase with indication of cell plate, observed at 5:00 P.M.; *f*, nuclear and cell division complete with transverse wall complete, at 5:30 P.M. Series C: *a*, anaphase as seen at 3:00 P.M.; *b*, late anaphase observed at 3:10 P.M.; *c*, telophase with cell plate forming at 3:25 P.M.; *d*, division of cell complete with transverse wall formed, at 3:45 P.M. Vacuoles can be seen developing in the tip of the cell.

that the chromosomes are not perfectly homogeneous structures but that at least two materials may be discerned. There appears to be a structural basis containing denser portions apparently of various shapes, often spirals (Fig. 93). The investigators realize the difficulties of determining the exact structure of a chromosome because of the action of the chemicals used in the preparation of the microscopic mounts.

Whether or not the chromosomes retain their individual identity from one cell division to another is a question which has attracted considerable attention. There is much evidence to support the idea that chromosomes do actually retain their individuality throughout the series of somatic divisions and from one generation of an organism to another. In certain plants with very small chromosomes the chromosomes may be seen even in the resting stage. In others where the divisions follow in quick succession, with only a very short resting stage, the chromatic material may not form a complete network. In such cases, the chromosomes do not lose their identity but may be observed throughout the resting stage. Even in those cases where the network or reticulum of chromatic material is formed in the resting stage, it is thought that the breaking down of the network during the early prophase occurs at the natural boundary of the original chromosomes entering into the formation of the network. It may be added that a vast amount of experimental data on the inheritance of characters in plants and animals supports the idea of the continuous identity of chromosomes from generation to generation through all cell divisions.

Direct Nuclear Division or Amitosis.

This method of nuclear division is rather unusual and seems to occur only in degenerating cells or in cells with a special nutritive function. The essential feature of amitosis is the division of the nucleus during the resting stage by constriction at or near the middle portion. In this process there is no organization of chromosomes, no spindle, and no wall formation. The nucleus is simply squeezed in two by the constriction. In cases of amitosis, the two nuclei are not separated by a cell wall, but the cell remains in the binucleate condition. Since amitosis takes place generally in cells which are degenerating, it is needless to do more than state that the process does not occur to any extent in growing tissue.

REGIONS OF CELL DIVISION—MERISTEMS

In many of the lower plants in which there is little or no tissue specialization, cell division may occur irregularly throughout the plant. Con-

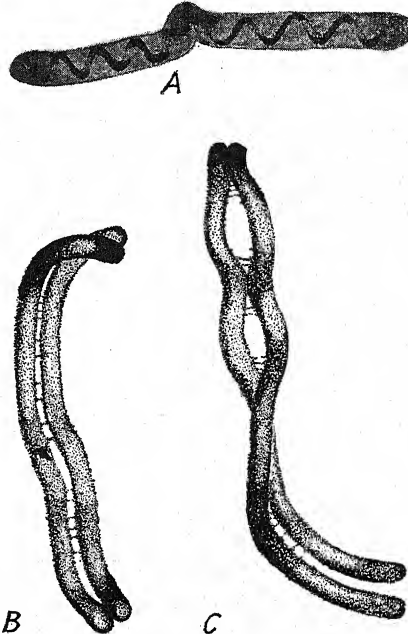


FIG. 93. Chromosome structure. A, chromosomes from lily microspore mother cell at reduction division, a spiral chromonema in each of the two chromosomes; B and C, chromosomes splitting as seen in the metaphase of a mitotic division. (A, from a slide prepared by O. P. Bollinger.)

sequently, such plants have no organs comparable with the roots, stems, and leaves of higher plants. In all multicellular plants in which there are specialized tissues, the formation of new cells by division is localized in rather definite regions called **formative regions**, or **meristems**. Attention has already been called to the meristematic regions in previous chapters. It should be emphasized here that all the permanent tissues of plants are derived from one or another of these meristems. Consequently, all the tissues of a plant may be classified as being either meristematic or permanent. The meristems of plants, in general, are the

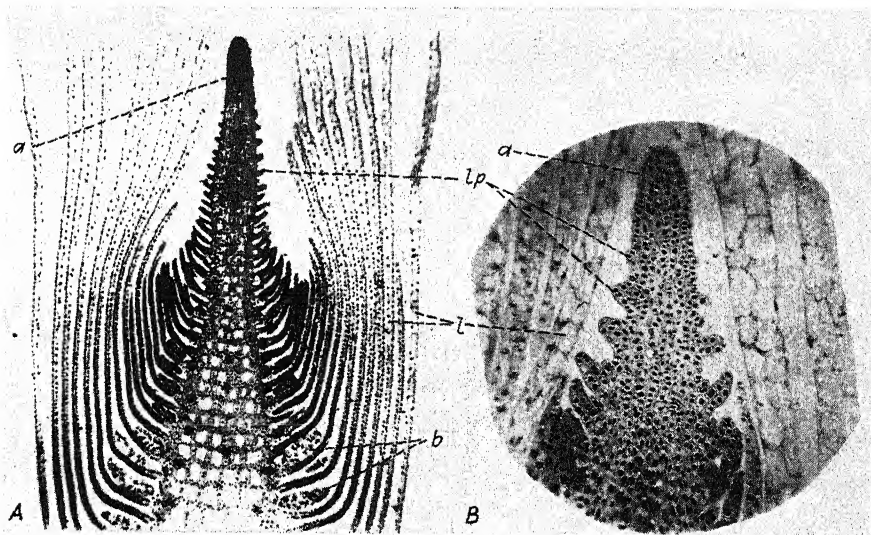


FIG. 94. Growing stem tip of *Elodea*. B, enlarged view of the terminal portion of A; a, apical meristem; lp, leaf primordia; l, leaves; b, axillary buds.

regions in which cell division takes place. They are the regions, therefore, where growth of a multicellular organ is initiated and from which all the tissues of the plant directly or indirectly originate.

Classification of Meristems. According to their position, meristems may be classified as **apical**, **lateral**, and **intercalary**. **Apical meristems** (Figs. 45, 60, 94) are those found at the tips of roots and stems, where they are commonly called **growing points**. They are responsible for the growth in length of the organs possessing them. In many of the lower vascular plants, the apical meristem consists of a single cell called the **apical cell**. In the seed plants, this tissue is made up of a group of cells. **Lateral meristems** are those situated along the sides of the stem and the root. The principal lateral meristems are the **vascular cambium** and the **cork cambium**, or **phellogen**. Lateral meristem cells divide

chiefly in one plane and thus cause the stems and roots in which they occur to increase in diameter. They are found chiefly in dicotyledonous plants and in gymnosperms. **Intercalary meristems** are parts of apical meristems which become separated from the apex by permanent tissues as the apical meristem moves forward. They are usually found at the bases of the uppermost internodes of the stems of many monocotyledonous plants (Fig. 53, *B*) and in *Equisetum*. In many plants they also occur at the base of the leaf. Like the apical meristems they function in increasing the length of the organ in which they occur. Unlike other meristems they ultimately wholly disappear as they are transformed into permanent tissues.

Primary and Secondary Meristems. Meristems may also be classified as **primary** and **secondary**. The **primary meristems** are those which persist from the time of their original development in the embryo or young plant in the seed. The principal primary meristems are the apical meristems of stems and roots and the fascicular cambium of dicotyledons and gymnosperms. The intercalary meristems of the monocotyledon stem are also primary meristems. Meristems that arise from permanent tissues are called **secondary meristems**. The most common secondary meristems are interfascicular cambium and the cork cambium, or phellogen. Both of these cambiums arise from cells that are already mature, the interfascicular cambium from parenchyma cells lying between the original primary vascular bundles, and the cork cambium from the epidermis, cortex, phloem, or pericycle. Other secondary meristems may arise in any part of the plant as a result of wounding or from other causes. Any living parenchyma cell is potentially able to develop into a secondary meristem. It is from such meristems that many abnormal growths, such as galls and tumors, develop. Such structures are often initiated by growth substances, which are described later in the text, and are often caused by insect injuries or by parasitic bacteria or fungi.

The primary meristems of seed plants, and particularly the apical meristems, originate in the embryo within the seed. In many seeds the entire embryo is in a meristematic condition. In others the apical meristems have already been developed at the tip of the rudimentary stem and the tip of the rudimentary root of the embryo. These apical meristems, as well as the principal lateral meristems, persist throughout the life of the plant, causing stems and roots to increase in length and in diameter. The meristems which give rise to leaves (leaf primordia) and the intercalary meristems of the stems of monocotyledons and a few other types of plants have a limited duration. As soon as the organs to which they give rise are formed, such meristems become completely transformed into permanent tissues and therefore cease to exist.

CELL ENLARGEMENT AND DIFFERENTIATION

Enlargement. When a cell divides, the two daughter cells together are at first only as large as the parent cell. Before growth can actually take place, the daughter cells must enlarge. Growth therefore includes not only cell division but also cell enlargement. In most of the meristematic regions of the plant, at least one of the daughter cells retains its meristematic condition and continues to divide. It is for this reason that such meristematic regions are perpetuated. The other daughter cell may also divide several times, but ultimately the cells arising from these divisions develop into permanent cells of one form or another. In regions where elongation is occurring, it is the daughter cells nearest the apex that remain meristematic. The elongation of the other daughter cells causes the apex to move forward. In the division of cambium cells, one of the daughter cells remains cambium and the other, either directly or after one or more divisions, develops into permanent cells.

The enlargement of the cells following division may take place in all dimensions or chiefly along one axis. The majority of the cells of such tissues as pith and cortex and the mature parenchyma cells of other tissues result from approximately equal expansion in all dimensions. Fibers, tracheids, sieve tubes, and vessels are formed by the greater enlargement of the lengthwise axis of the cell. The shape and final form of all cells of permanent tissues are determined by the manner of enlargement of the original daughter cells resulting from division.

The enlargement itself results from the synthesis of new substances within the protoplasm and by the absorption of materials from adjacent cells or from the exterior. The first of these is sometimes called **growth by accretion**. The new materials synthesized often consist of hydrophilic colloids and osmotically active substances. These substances cause the cell to absorb water and therefore to stretch out. The expansion of the cell resulting from such absorption is called **growth by distension**. As the cell expands, the cell wall is thickened by the addition of new material, chiefly cellulose, made by the protoplasm. Usually the protoplasm itself, although it does increase in volume, does not keep pace in its growth with the increased size of the cell. In the original meristematic cell, the protoplasm occupies practically the entire cavity of the cell. As the cell grows, the vacuoles increase in size and many of them coalesce until finally there may be one large central vacuole with the protoplasm occupying a peripheral position in the cell.

Maturation. As the cells enlarge, they gradually assume their permanent shapes and forms. This final phase of growth is usually called **maturation**. As maturation proceeds, the cells become fully differentiated. While all the cells are alike in the meristematic condition, their shapes,

forms, and functions when they are fully differentiated are quite varied. The volume of the cell may have increased a hundred or a thousand times. The cells may remain living in the mature condition or may die. They may remain parenchyma cells or become sclerenchyma, collenchyma, or highly differentiated xylem vessels, or sieve tubes. It is during the maturation phase of growth that all the different kinds of cells and tissues that have been described in the chapters on the leaf, the root, and the stem are developed.

Primary and Secondary Tissues. The permanent cells that develop directly from the apical meristems are called primary tissues; those developed from cambiums are called secondary tissues. Primary and secondary tissues have already been considered in the chapters on the stem and the root and need not be taken up here.

FACTORS AFFECTING GROWTH

The rate at which a plant or an organ grows, as well as the shape or form it assumes, is determined by the combined operation of a multitude of complex internal and external factors. Internal factors are conditions existing within the plant, while external factors are conditions of the surroundings or environment of the plant. As stated by the German botanist Klebs, we may look upon a plant bud as a group of possibilities or potentialities, and what it becomes depends upon the factors brought to bear upon it. Of these factors, those which are external or environmental are more readily brought under control and hence have been more widely investigated. Relatively little is known concerning the internal factors. In the pages that follow, only a brief treatment can be given of the manner in which some of these factors operate.

INTERNAL FACTORS

Among the internal factors that affect growth may be mentioned **heredity**, the presence of **growth-regulating substances**, including **hormones**, **vitamins**, and other physiologically active substances occurring in minute quantities, the general **nutritional balance** of the plant, and the **correlation of plant parts**.

Heredity. It is the heredity or inheritance of the plant that gives it its potentialities for developing into a certain form. Each plant has a group of hereditary factors which are capable of influencing the development of definite characters, provided the proper conditions are supplied to bring these characters out. For example, when the Peking variety of soybeans is grown in light from which the blue-violet end of the spectrum has been eliminated, the plants become twiners (Fig. 100, *B*). Four-o'clocks, on the other hand, although they grow unusually tall, do not become

twiners under the same conditions. The difference between these two species in their response to this environmental condition rests upon the fact that the soybeans have a hereditary factor for twining, while the four-o'clocks apparently do not. The Peking soybeans do not twine, however, under ordinary light, which shows the importance of environmental factors in bringing out hereditary characters. Many of the general hereditary characters of plants, however, appear so constantly that even extreme variations in environmental factors fail to change them. A germinating bean seed, for example, cannot be made to develop into a pea plant or into any other kind of plant, no matter what environmental factors are brought to bear upon it. It is for this reason that species remain fairly constant under all conditions. Most of the structural and other distinguishing features of species are caused by hereditary factors that usually cannot be changed except by breeding. Heredity is therefore one of the most important factors affecting growth and development in the plant.

Nutritional Balance. The relative proportions of the foods—carbohydrates, fats, and proteins—in the plant body probably have much to do with the type of growth the plant makes. A "balanced ration" may be as necessary for the plant as it is for the animal. Since green plants synthesize all these foods themselves, the nutritional balance is conditioned by the supply of inorganic salts available to the plant as well as by the factors that influence photosynthesis. The importance of a proper balance between carbohydrates and nitrogen compounds in the plant has received the greatest attention of investigators. Thus it has been shown that when tomato plants are supplied with an excess of nitrate and an abundance of water, under ordinary conditions of light, they are likely to become excessively vegetative and unfruitful. In this case, there is relatively too much soluble nitrogen in proportion to the amount of carbohydrate present to induce flowering and fruiting. On the other hand, if nitrogen is withheld from the plants, without preventing photosynthesis from taking place, *i.e.*, by keeping the plants in good light, carbohydrates may accumulate in great quantities because they are not used in the synthesis of proteins and other nitrogenous substances, and the plants become very short and tough, nonvegetative and nonfruitful. They also become nonvegetative and nonfruitful, short and weak, when supplied with an abundance of nitrogen in the absence of sufficient light for active photosynthesis, in which case the carbohydrates are too low in quantity to permit the synthesis of higher organic compounds necessary for growth. Between these extremes there exists a condition of balance between the amount of carbohydrate and the quantity of nitrogen compounds in the plant under which they become both vegetative and fruitful. This

condition, obviously most desirable from the grower's viewpoint, is found when the plants are kept in good light and are supplied with a moderate amount of soluble nitrogen compounds.

The same correlation between a proper balance between carbohydrates and nitrogen compounds and growth and fruiting has been reported with other plants. Other relationships between foods and other compounds in the plant may also be effective in growth, but little is known about them.

Growth Substances. *Hormones.* **Hormones** are substances which, though produced by the organism in extremely minute quantities, are capable of producing profound physiological effects. In the animal body they are sometimes referred to as "chemical messengers" because they are produced in one organ and are carried in the blood stream to another organ upon which they have their effects. Well-known examples of hormones found in the animal body are thyroxine, epinephrine, and insulin. None of these have been found in plants. Plant hormones, or **phytohormones**, have been shown to play a prominent role in the growth of plants, influencing root and stem growth, the elongation of cells, the production of flowers, movement of organs, the dominance of certain parts of plants over others, and the production of many abnormal growths, such as galls and tumors. In addition to the true hormones, many synthetic compounds, such as indolebutyric acid, α -naphthaleneacetic acid, α -naphthalene acetamide, and many others produce similar effects on plants. The general term **growth-regulating substances**, or simply **growth substances**, may be applied to all such substances as well as to the plant hormones and vitamins.

Prominent among plant growth substances are the **auxins**, which are considered to be essential for normal growth in length and to be effective physiologically in other ways. They have been found in the growing tips of stems, in pollen, in seeds, in leaves, and in other organs of the plant. They are found particularly in apical meristems and cambiums. Since they occur in extremely minute quantities, ordinary chemical methods cannot be used for their determination. One of the earliest methods used for auxin determination is the so-called *Avena* test, in which young seedlings of oats (*Avena sativa*) are used. In the very young oat seedling, the growing shoot is surrounded by a sheath called the coleoptile. If 1 or 2 mm. of the tip of the coleoptile are cut off, the coleoptile no longer elongates at a normal rate. Placing the tip back on the cut coleoptile restores the normal rate of elongation. If the tip is placed on only one side of the cut surface of the coleoptile, the side on which it is placed grows more rapidly than the other side, causing the coleoptile to bend away from the side to which the tip was applied. This indicates that something produced in the tip is transported downward into the

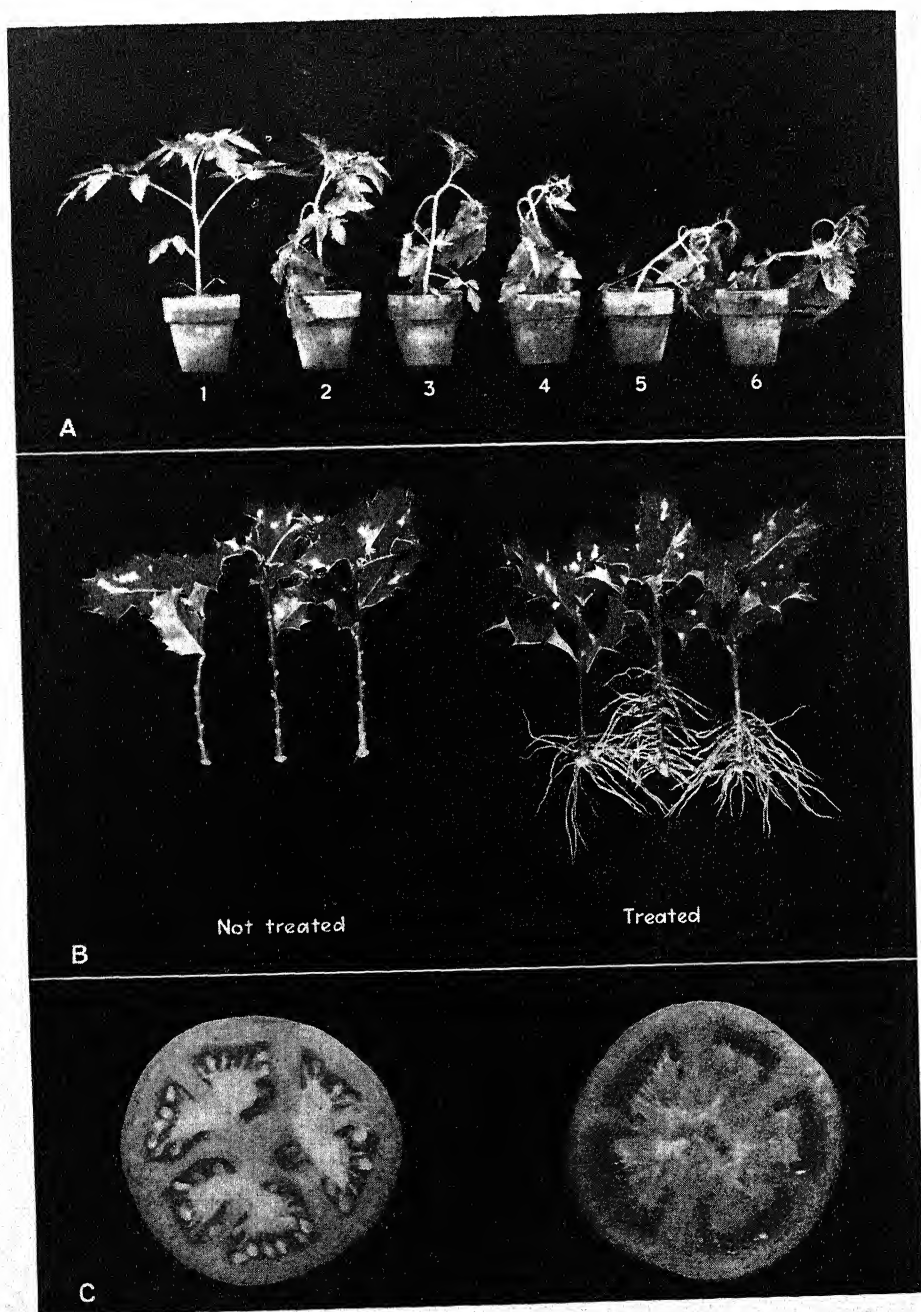


FIG. 95, I. See legend at bottom of next page.

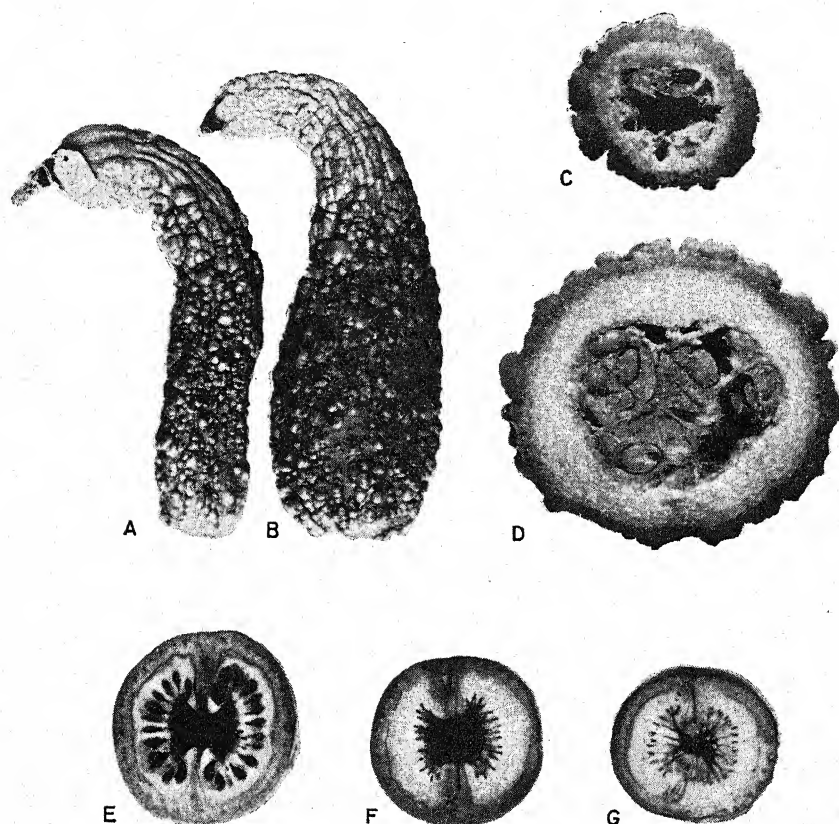


FIG. 95, II. Effects of growth substances (continued from Fig. 95, I). A-D, crook-necked summer squash; A, parthenocarpic fruit produced by application of indolebutyric acid to the style of an unpollinated flower; B, a normal fruit resulting from pollination; C, section of the fruit shown at A; D, section of the fruit shown at B; note seeds in D and absence of seeds in C; E-G, yellow plum tomato; E, control showing seeds resulting from pollination of the flower; F and G, parthenocarpic fruits induced by spraying the flowers and buds with β -naphthoxyacetic acid (50 mg. per liter). (A-D, from photographs furnished by Dr. Felix G. Gustafson, University of Michigan; E-G, from a photograph furnished by Dr. P. W. Zimmerman, Boyce Thompson Institute for Plant Research, Inc.)

FIG. 95, I. Effects of growth substances. A, bending of stems and leaves of tomato resulting from treating one side of the stem with α -naphthaleneacetic acid in lanolin; 1, treated with lanolin only; 2-6, treated with 0.05, 0.1, 1.0, 5.0, and 10.0 mg. of α -naphthaleneacetic acid per gram of lanolin respectively; note epinasty (downward bending) of leaves; B, English holly (*Ilex aquifolium*) showing roots induced by treatment with indolebutyric acid; untreated controls on left failed to root; C, fruit of Bonny Best tomatoes; left, control untreated, showing development of seeds following pollination; right, parthenocarpic (seedless) fruit developed after the flower cluster was treated with *o*-chlorophenoxypropionic acid, 50 mg. per liter. (Photographs furnished by Dr. P. W. Zimmerman, Boyce Thompson Institute for Plant Research, Inc.)

coleoptile and affects its growth. If the tips of such coleoptiles are cut off and placed cut surface down on an agar gel for some time, some of the growth-promoting substance (auxin) diffuses out of the tips into the agar. If now a small cube of the agar is cut out and placed on one side of the cut surface of a coleoptile from which the tip has been removed, a bending of the coleoptile takes place away from the side to which the agar block was applied, indicating that the auxin has now diffused out of the agar into the side of the coleoptile to which it was applied, causing that side to grow more rapidly and thus causing a bending. Similarly, if the growing tips of other plants are placed on agar in this manner, auxins will diffuse into the agar and tiny cubes of this agar will cause bending of decapitated coleoptiles. It has been found that, within limits, the degree of bending of the coleoptile is proportional to the amount of auxin present in the agar cubes. By measuring the degree of bending, it is possible to determine the amount of auxin present in the agar. This method furnishes a means of measuring quantitatively the amount of auxin which diffuses out of plant parts. In practice, it is necessary to control temperature and in other ways to standardize the method of procedure. Since the coleoptiles bend toward light, it is necessary to keep them in darkness during the procedure. It has been estimated that 1 part of a naturally occurring auxin from a stem tip in 110 million parts of water causes a bending of 10° in an oat coleoptile.

Auxins can also be extracted from plant tissues with chloroform or ether. In water extracts made at ordinary temperatures, the auxins are rapidly inactivated by oxidizing enzymes. One of the auxins, called heteroauxin, is indoleacetic acid. Since this can be obtained in a pure form, auxin activity can be compared quantitatively with that of pure indoleacetic acid.

Growth substances (Fig. 95, I, II) are considered to be effective not only in stem elongation but also in the abscission of leaves and fruits, in the dominance of apical buds, in fruit development, in the initiation of roots on stems, and in tropisms, as is shown later in the text. They are also thought to be effective agents in causing abnormal growths such as the galls caused by insects, and tumors caused by fungi and bacteria. Such overgrowths have been produced experimentally by injecting growth substances into plant tissues. The root nodules of the legumes are also thought to be caused by growth substances. The use of growth substances in the rooting of cuttings has become an established practice. Often cuttings of hardwoods that do not root readily can be made to root if treated with growth substances. They are also used in a practical way to prevent the pre-harvest dropping of fruits such as apples. In fruits sprayed at the proper time with synthetic growth substances, the development of the abscission

layer is delayed. The setting of fruit in the tomato has been enhanced, and the production of seedless fruits in a number of plants has been accomplished by the use of growth substances. Also, 2,4-dichlorophenoxy-acetic acid, often classed with growth substances and commonly referred to simply as 2,4-D, has come into prominence as a weed killer.

The exact mechanism of the action of growth substances has not yet been determined satisfactorily. There is some evidence that they may affect respiration, enzyme activation, and perhaps other physiological activity. For normal growth of a plant, there must be an adequate supply of food, *i.e.*, carbohydrates, fats, and proteins. These are the building materials and must be present in comparatively large quantities. The growth substances, which occur in minute quantities, might be thought of as exercising the control over the utilization of these building materials and perhaps affecting their actual incorporation into the structure of the plant body.

Vitamins. The **vitamins** are a group of organic substances that have been shown to have profound effects on the growth and health of animals. Since they were originally shown to be essential constituents in the diet of animals, although occurring in minute quantities, they were called at first "accessory foods." Since they were obtained by the animal in foods, they were thought of as exogenous substances as opposed to hormones, which were endogenous, *i.e.*, produced within the body of the organism. This distinction does not hold with plants, since most green plants apparently are able to synthesize vitamins within their tissues. Hence, it is sometimes difficult to distinguish between vitamins and hormones in the plant. Vitamins were defined by Willaman as "a class of substances, the individuals of which are necessary for the normal metabolism of certain living organisms but which do not contribute to the mineral, nitrogen, or energy factors of the nutrition of these organisms." By not contributing to the energy factors of nutrition, Willaman undoubtedly meant that the vitamins are not oxidized by the organism for their contained energy as are the foods. Some of them, such as thiamin, nicotinic acid, and riboflavin, definitely take part in energy transfer which occurs in oxidative metabolism, *i.e.*, in respiration. Although they are identified with the nutrition or metabolism of organisms, the vitamins, like the hormones, are effective in minute quantities and can be looked upon as growth substances. They are not foods. Unlike enzymes, the vitamins are used up by the organism. Many of them are definite chemical compounds that have now been synthesized artificially.

It has been known for a long time that plants are the principal source of most of the vitamins needed by animals but only comparatively recently has it been shown that they are essential to the life of plants. Among the

important vitamins that are synthesized by plants and that probably take part in the metabolism and growth of plants are the following: *vitamin A*, a fat-soluble vitamin derived from carotene and essential for normal growth and vision of animals; *B₁*, or *thiamin*, the water-soluble antineuritic or antiberiberi vitamin; *B₂*, or *riboflavin*, a water-soluble growth vitamin; *nicotinic acid*, *pyridoxine*, or *B₆*, and *pantothenic acid*, all of which are members of the water-soluble B group and are the pellagra-preventative vitamins of humans, rats, and chicks, respectively; *biotin*, *inositol*, and *p-aminobenzoic acid*, which are also members of the water-soluble B group of vitamins; *vitamin C*, or *ascorbic acid*, the water-soluble antiscorbutic vitamin; *vitamin D₂*, or *calciferol*, the fat-soluble antirachitic vitamin; *vitamin E* or *α -tocopherol*, the fat-soluble antisterility vitamin; *vitamin K*, a fat-soluble antihemorrhagic vitamin, and *vitamin P*, a flavone derivative concerned with permeability.

The effects of vitamin deficiency in animals are studied by withholding vitamins from the diet. With many autotrophic plants, this method is not possible because such plants make their own foods and usually can also synthesize all the vitamins they need. Some of the fungi, however, are unable to synthesize certain vitamins. Roots and certain tissues of higher plants may depend upon other organs of the plant for their source of vitamins. Thus much of our knowledge of the importance of vitamins to plants has been obtained by studies with fungi, with isolated embryos or root tips, or with tissue cultures of higher plants on synthetic media.

From the culture of isolated root tips on synthetic media it has been demonstrated that vitamin *B₁*, or thiamin, is essential for the growth of roots *in vitro*. Thus, when a short root tip of a pea plant is cut off and transferred to a suitable medium containing the necessary inorganic substances and sugar, it will grow for a time at a comparatively fast rate. If now the tip of this root is removed and transferred to a fresh nutrient solution made up of inorganic substances and sugar, it will grow very little, and a third transfer may result in complete cessation of growth. If, however, a small amount of vitamin *B₁* is added to the nutrient solution, the severed root tip will continue to grow at a fast rate. Obviously, the original root tip contained enough vitamin *B₁*, which it received from the aboveground parts of the plant, to enable it to continue growth, but when it was used up, further growth was checked unless vitamin *B₁* was supplied to the nutrient medium. This indicates that the root tip is unable to synthesize vitamin *B₁* but must depend upon the aboveground parts of the plant for its supply. Examination of root tips that have failed to grow because of lack of vitamin *B₁* indicates that cell division has ceased. Thus it is shown that cell division in root tips depends upon a supply of vitamin *B₁*. Many other roots give the same response to vitamin

B₁, but roots vary in the amount of this vitamin which is available to them while they are still attached to the plant. With most plants, an adequate amount is available, and therefore the supplying of additional vitamin B₁ to the roots of growing plants is often without effect. Some roots require for normal growth not only thiamin but also nicotinic acid and pyridoxine. There is apparently a diversity of vitamin requirements of roots of different kinds of plants.

Cultures of embryos detached from seeds, with cotyledons and endosperm removed, have also been made. Various workers have reported the need of such vitamins as thiamin, biotin, and ascorbic acid by embryos of different plants cultured in this manner. Studies of this type as well as other tissue cultures of higher plants have demonstrated the importance of vitamins to such plants.

Some of the earliest work on the relation of vitamins to plants was carried out with fungi, particularly with yeasts. Studies with fungi have been particularly enlightening. Some of the fungi apparently are able to synthesize all the vitamins they need for normal growth. Others, however, are distinctly limited in this respect and will not grow well unless they are furnished with certain vitamins in the culture medium. Thus, *Phycomyces blakesleeanus*, a simple mold, cannot synthesize thiamin and will not grow unless this vitamin is supplied in the culture medium. Chemically, the thiamin molecule is made up of two simpler substances, thiazole and pyrimidine. *Phycomyces* will grow if supplied with these two substances but not if only one or the other is supplied. Other fungi can synthesize thiamin if supplied with thiazole only, while still others can do so if supplied with pyrimidine only. Other vitamins that have been shown to be necessary for certain fungi include biotin, pantothenic acid, nicotinic acid, pyridoxine, and inositol. Wide differences apparently exist among the fungi in their requirements for different vitamins.

Some of the fungi have been found useful for vitamin bioassays, *i.e.*, for the determination of the amount of certain vitamins present in foods or plant tissues. Such fungi have complete deficiencies for a given vitamin, and the amount of growth they make in a given time is proportional to the amount of this particular vitamin available to them. By measuring the amount of growth of such fungi in a culture medium to which is added a definite quantity of food or tissue, the vitamin content of which is to be ascertained, the vitamin content of the food or tissue can be determined. Thus certain races of yeast can be used for pyridoxine determination. *Phycomyces blakesleeanus* can similarly be used for vitamin B₁ assays.

The functions of many of the vitamins in plants have not yet been determined. Vitamin B₁ and possibly other members of the B group of vitamins probably operate through their relationship to vital enzyme

reactions concerned in respiration. Some of them have been shown to be coenzymes. They are often very specific in their action and are sometimes effective in extremely minute amounts. Thiamin, for example, in some cases has been reported to be still active in a dilution of one part in 40 trillion. One gram of biotin dissolved in 25 million gallons of water has been found to be sufficient for the normal growth requirement of yeast and of certain bacteria. The exact conditions under which they are synthesized in the plant likewise are not well known, although such environmental factors as light and the supply of inorganic substances have been shown to affect the content of certain vitamins in plants.

Correlation of Plant Parts. It has long been known that the removal of one part of the plant may affect the growth of other parts. Removal of the terminal parts of stems, for example, stimulates to growth lateral buds which normally would remain dormant. For this reason, it is often possible to change radically the shape and form of a plant by pruning. A similar relationship exists between the development of vegetative shoots and flowers. Thus, if the flower buds of tomato plants are pinched off as they appear, the plant is stimulated to renewed vegetative growth. On the other hand, if the fruits are allowed to develop, vegetative growth is checked. In most annual plants, the cessation of vegetative growth is correlated with the development of flowers and fruits on the plant.

Not only is the amount of growth an organ makes influenced by the removal of other organs but sometimes its whole form and structure as well. Thus the tendrils of pea leaves sometimes develop into broad leaflets if the foliage leaflets are cut away before the leaf has fully developed. Similarly, the highly modified sporophylls (spore-bearing leaves) of some ferns become vegetative leaves if the ordinary leaves are removed before the sporophylls are fully differentiated. Many other examples could be given.

The effect of removing organs on those that remain indicates that, in the normal growth of the plant, these organs must have a reciprocal influence on each other. The development of the vegetative shoot affects the development of roots; the growth of roots, in turn, affects that of the vegetative shoot; flower development affects vegetative-shoot development, and so on. Some of these effects have been attributed to the influence of hormones, but, in general, little is known as to how they are brought about. Undoubtedly competition among the different organs for the food supplies plays a part.

Periodicity of Growth—the Grand Period. The operation of internal factors is clearly manifested in the course of growth of a plant, as well as in the growth of any one of its parts, from the undifferentiated form to maturity. The growth of a cell, an organ, or a whole plant does not

proceed at a uniform rate even when the conditions under which the plant is growing are kept uniform. Growth starts at a slow rate, gradually increases until a maximum rate is reached, and then falls off until it finally comes to an end. This can readily be shown by measuring, at regular intervals, the size of a growing organ or plant from the beginning of its growth until it is mature and by plotting the increase in size against time. When this is done, a characteristically shaped curve is obtained similar to the one shown in Fig. 96, A. If the actual size of the organ or plant is plotted against time, an S-shaped curve is obtained as shown in Fig. 96, B. Such curves are obtained no matter what measurement of

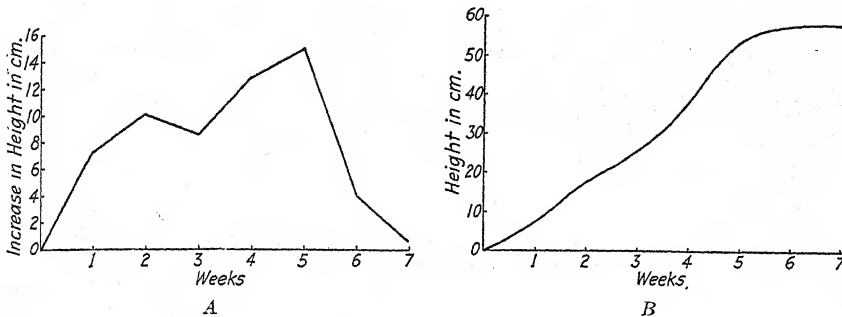


FIG. 96. Curves showing growth of Mandarin soybeans. A, increase in height plotted against time, giving a typical "grand period of growth curve." The drop in the curve during the third week represents approximately the period at which the seedlings had exhausted the reserve foods stored in the seeds and become independent plants. The drop during the sixth week is correlated with the initiation of flower production. B, the typical S-shaped curve obtained by plotting the actual height of these same plants against time. (Drawn by F. Brown from data by H. W. Popp, *Effect of Light Intensity on Growth of Soybeans and Its Relation to the Autocatalyst Theory of Growth*, *Botan. Gaz.*, 82: 306-319, 1926.)

size is used. Sudden fluctuations in temperature or in other environmental conditions may cause irregularities in the curve but, if the whole period of enlargement is included, the general shape of the curve will remain the same. The total period of enlargement of an organ or a plant is called the **grand period of growth**, and the first type of curve mentioned above is referred to as a grand-period curve.

External conditions may shorten or prolong the grand period or they may change the ultimate size of the plant but they have little or no effect on the course of growth as indicated. This fact has led to much speculation as to the underlying internal factors that bring it about. Most of the internal factors that have been mentioned, as well as others, have been individually championed by one investigator or another in explanation of it, but as yet no one of the explanations has met with general acceptance. The initiation of flowering, as mentioned in a previous section, has been definitely shown to be correlated with the falling off and

final cessation of vegetative growth. Other correlations of plant parts and general food relationships also probably play a part.

In perennial plants, periods of active growth are followed by periods of rest. In such plants, each active period of growth follows the course of a grand period. The periodicity of perennial plants is most pronounced in temperate and arctic regions but occurs also in many tropical species. The development of flowers and fruits and of other parts of the plant is also periodic in perennial plants. While periodicity may be influenced by external factors, it is probably governed largely by internal factors.

EXTERNAL FACTORS

GENERAL

The effects of external, or environmental, factors on growth have been much more thoroughly studied because of the fact that many of these factors are more readily brought under control and their effects more readily observed. In the last analysis, however, the operation of external factors cannot be separated from that of internal factors. Any change in growth that results from the operation of an external factor can be explained only on the basis of a change in the internal conditions of the plant. In other words, the mechanism of the action of external factors rests on the influence such factors have on the internal mechanism of the plant. It is in this manner that external factors may affect not only the rate of growth and the ultimate size of a plant or an organ but also its general form. Changes in general structure and form are usually referred to as **formative** effects. Many of the external factors have a formative effect on the plant. It should be emphasized that the actual growth of the plant results from the simultaneous operation of all factors, internal as well as external. It is therefore not always possible to separate the influence of a single factor from that of other factors.

Of the external factors influencing growth, **radiation, temperature, and moisture** have been most studied. The supply of **oxygen, inorganic salts, and carbon dioxide** is no less important. These have already been referred to in previous chapters. The oxygen supply influences the respiration of the plant and through it, growth. It is considered in Chap. 12 and need not be taken up further here. The carbon dioxide supply affects photosynthesis, which in turn affects all organic synthesis within the plant and hence growth. It has already been considered in Chap. 5. The effect of inorganic salts has been briefly taken up in Chap. 7. While it is definitely known that many of these salts are necessary for growth, the exact manner in which many of them influence growth has not been satisfactorily determined. A detailed discussion of their possible

influences would be too involved in a work of this kind. Electricity, gravity, mechanical agents, insect and fungus injuries, and the presence of toxic and stimulating substances in the environment also affect growth. The present discussion is restricted more or less to radiation, temperature, and moisture.

RADIATION

Importance of Radiation. Probably no other environmental factor in nature plays a more important role in the growth of higher plants than does radiation, and particularly visible radiation or light. It is the ultimate source of all energy stored by the plant in photosynthesis, upon which all forms of life are directly or indirectly dependent, and without which all growth would ultimately cease. Light affects the germination of some seeds. After the young plant has emerged from the seed, its future is again influenced by the kind and amount of radiation it receives. Not only is the rate of growth of the plant conditioned by the environmental radiation, but the size and form, the internal structure, the composition, the intensity of internal physiological processes, flowering, fruiting, and seed development of the plant are affected as well. The movement or orientation of plants and plant organs and the distribution of plants are likewise influenced by radiation. In short, radiation is a constant and important factor in the life of the plant from germination to maturity. It probably exerts a greater formative effect on plants than does any other external factor.

Variability of Radiation. The universal source of radiation of plants in nature is the sun. Much of the radiation from the sun is scattered by dust particles and moisture in the atmosphere. This diffused skylight is different in quality and intensity from direct sunlight. The combined radiation from the sun and the sky is commonly referred to as daylight. Both the quality and the intensity of daylight vary from hour to hour even on perfectly clear days. The intensity gradually increases from morning to noon and decreases from noon to night. The variation in quality is manifested by the difference in color of sunlight in early morning or late evening as compared with noon. Quality, intensity, and duration of daylight (length of day) also vary with the season of the year. On cloudy days quality and intensity may vary from minute to minute and over a wide range. These wide variations have made it difficult to study the effects of radiation on plant growth. Artificial light sources have been used for plant studies, but the radiation from these also varies widely. Furthermore, no artificial source has yet been found which approximates the quality and intensity of noon daylight in summer.

Sunlight consists of infrared, visible, and ultraviolet radiation. Its spectrum extends from about 5,000 $m\mu$ in the infrared down to 291 $m\mu$ in the ultraviolet (1 $m\mu$ = one-millionth mm.). The region of highest energy value in this spectrum is usually in the yellow to green region. The energy falls off gradually toward the infrared and rather sharply toward the ultraviolet. For the sake of comparison with other

types of radiation, the approximate limits of different regions of the electromagnetic spectrum are given in the following table:

THE ELECTROMAGNETIC SPECTRUM

Radio waves.....	2,000,000 to 5,000 cm.
Short electric waves.....	5,000 to 0.025 cm.
Infrared (heat).....	320,000 to 720 m μ
Visible region (light).....	720 to 400 m μ
Red light.....	720 to 626 m μ
Orange light.....	626 to 595 m μ
Yellow light.....	595 to 574 m μ
Green light.....	574 to 490 m μ
Blue light.....	490 to 435 m μ
Violet light.....	435 to 400 m μ
Ultraviolet.....	400 to 13.6 m μ
X rays.....	1.32 to 0.007 m μ
Gamma rays of radium.....	0.137 to 0.002 m μ
Cosmic rays.....	Less than 0.002 m μ (?)
Sunlight spectrum.....	5,000 to 291 m μ

It should be emphasized that no one source of radiation consists of any more than a limited region of the whole electromagnetic spectrum. Furthermore, the energy distribution in the spectrum of any two sources of the same range may be widely different. It is the spectral range and the energy distribution that are meant when quality of light is mentioned. Each region of the spectrum may affect plant growth. In the pages that follow, reference is made to effects of intensity, quality, and duration of radiation, with special emphasis on visible radiation or light.

Effect of Darkness—Etiolation. Long before anything was accurately known concerning the effect of light on plants, the abnormal development of plants in darkness had been observed. The general appearance of plants grown in the total absence of light is familiar to everyone. In most dicotyledonous plants, darkness causes excessive elongation of stems (Fig. 97), brought about chiefly by the abnormal lengthening of internodes. Petioles are also unusually long, but leaf blades small and undeveloped. The complete absence of chlorophyll gives the plants a pallid or yellow color. Rosette plants, which in light have unusually short stems, sometimes develop upright stems in the dark. In monocotyledons, the leaves but not the stems become abnormally long in darkness (Fig. 97, *C, D*), but the leaves are usually very narrow. Roots are usually poorly developed in all plants grown in the dark. Plants grown from seed fail to develop flowers in the dark but, when grown from buds in which flower primordia have been developed, such plants may produce flowers in the dark. The flowers in this case are usually paler in color. Many other abnormalities occur in specialized organs.

The tissues of plants grown in darkness are unusually soft, weak, and succulent. Cells are large, thin-walled, and relatively undifferentiated.

Strengthening tissues are poorly developed. Leaf mesophyll is of a homogeneous, loose structure with little differentiation of palisade and vascular tissue. As compared with plants grown in light, the dry weight of such plants is considerably lowered, and the percentage of water increased. Sugars and soluble nitrogen compounds are usually higher in plants grown in the dark.

Plants having the characteristics enumerated above are said to be **etiolated**. The ability of etiolated plants to survive in the dark depends



FIG. 97. A-B, effect of darkness upon a dicotyledonous plant, the common bean (*Phaseolus vulgaris*); A, grown in weak, diffused light; B, grown in darkness; both planted at the same time; C-D, effect of darkness upon monocotyledonous plants, wheat (*Triticum sativum*); C, grown in darkness; D, grown in weak, diffused light.

partly upon the quantity of stored foods available to them. Plants grown from storage roots, tubers, bulbs, or corms usually live longer in the dark than do seedlings. Unless light is provided, all higher plants sooner or later die. Death is hastened at high temperatures because of the rapid consumption of the food reserves brought about by increased respiration. It is interesting to note also that even a very small amount of light may profoundly influence the development of etiolated plants. Thus it has been shown that as little as 2 min. of light per day is enough to cause etiolated seedlings of peas and broad beans (*Vicia Faba*) to start to expand the growing tip (plumule) and to unfold leaves which otherwise would not have developed in the dark.

The cause of etiolation is not yet fully known although it seems to be definitely tied up with the activity of growth hormones. That it is not caused by the failure of photosynthesis to take place is proved by the fact that plants grown in light but in the absence of carbon dioxide do not become etiolated. A type of etiolation is sometimes produced in plants grown at high temperatures or in the absence of the blue-violet end of the spectrum or in very weak light of any kind. Respiration and catabolic metabolism, in general, seem to proceed at a rapid rate in etiolated plants. The plants elongate rapidly as though they were reaching out for light. It is also interesting to note that leaves, which can function only in light, are usually not well developed in the dark. These features, though in no sense causal, are of some advantage to a seedling growing from seed lying deep in the soil. Etiolation caused by darkness occurs also in gymnosperms, lower vascular plants, mosses, algae, and fungi.

Effects of Intensity of Radiation. The effect of low light intensity is similar to that of darkness in that it causes excessive elongation of stems, but it differs markedly in the effect it has on leaves and on chlorophyll development. Even in weak light, leaves completely unfold and develop an abundance of chlorophyll but remain thin and poorly differentiated internally. Leaves grown in dense shade have a loose palisade tissue consisting of a single layer of cells and a very loose spongy mesophyll, filled with air spaces. The epidermis is not heavily cutinized. The other tissues of the plant are also weak and tender. Roots are poorly developed when the tops of plants are in weak light.

As the light intensity is increased, the stems become shorter, there is a better development of roots, and all tissues are better differentiated. The plant takes on its ordinary appearance. Leaves reach a maximum size in moderate intensities. The final height attained by the plant is also often greatest in a medium intensity of light (Fig. 98). At very high intensities many plants remain very short and stocky. The leaves are likely to be smaller in area but much more compact and thicker. Often there are two or more palisade layers and very few air spaces even in the spongy mesophyll. High light intensity is conducive to a higher transpiration rate. All the structures enumerated tend to reduce this loss. The stems of plants grown under high light intensity are much thicker and the strengthening tissues are more fully developed. Within limits, the higher the light intensity, the greater is the dry weight of the plant. Roots and general storage organs are always better developed and flowering and fruiting are at a maximum in strong light. In very weak light, flowering and fruit development sometimes fail to occur altogether. The ratio of roots to tops of plants usually increases with increased light. The greater sturdiness of plants grown in full sunlight is probably caused in part by

the increased photosynthesis under this condition. Shade plants are often low in carbohydrates and high in nitrogen compounds as compared with sun plants. The checking effect of light on stem elongation accounts for the fact that most plants grow more rapidly at night than they do during the day.

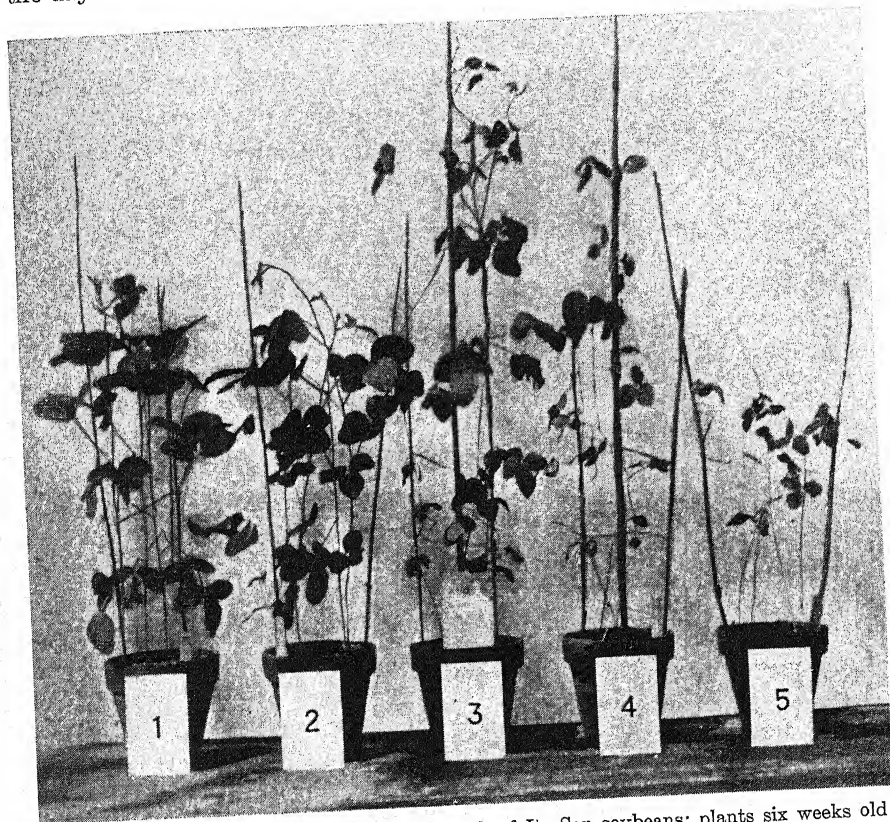


FIG. 98. Effect of light intensity on the growth of Ito San soybeans; plants six weeks old; approximate percentage of full daylight intensity received by each plant: 1, 66 per cent; 2, 23 per cent; 3, 8.6 per cent; 4, 6 per cent; 5, 3.8 per cent. Note that the maximum height was attained by the plants under a medium light intensity (3). (From H. W. Popp. *Effect of Light Intensity on Growth of Soybeans and Its Relation to the Autocatalyst Theory of Growth*, *Botan. Gaz.* 82: 306-319, 1926.)

Plants do not all respond in the same manner to light intensity. Some require more light than others. Some species, like the sunflower, grow best only in full sunlight. Others may be able to live in as little as one one-hundredth of the intensity of full sunlight. Only plants that have a relatively low light requirement can develop normally in dense shade. Partly for this reason, the species that are found growing under the canopy

of dense forests are limited. Similarly, light intensity is one of the factors determining the succession of different associations of plants in a given area. When a beech, maple, and hemlock forest is cut down and the area is left unplanted, it is not replaced in the immediate future by a forest of the same type. An entirely new association of plants invades the area. Most of these new plants are able to grow in direct sunlight. This new association may be replaced by several others before the area, after many years, gets back to the original beech-maple-hemlock forest. The latter is able to maintain itself indefinitely, however, if not burned or cut down, partly because the seedlings of these species are able to develop in the shade of the mature trees. An association of this type that is able to maintain itself is called a **climax association**. It should be mentioned that many other factors besides light determine succession and the maintenance of climax associations.

Effects of Quality of Radiation. The effects of different regions of the spectrum have been studied by growing plants under glasses that transmit limited regions. In all studies of this kind, it is important that intensities be kept equal under the different kinds of radiation; otherwise it is impossible to separate quality effects from intensity effects. From studies of this kind it has been found that plants grown under the red-orange part of the spectrum become etiolated even at high intensities, although they become green. Those grown under the blue-violet end of the spectrum more nearly resemble plants grown in the full spectrum of daylight. Most striking results have been obtained when plants were grown in daylight from which the blue-violet end of the spectrum below $529\text{ m}\mu$ was eliminated. Many plants grown from seed under this condition elongate more rapidly during the first two or three weeks of growth, as compared with plants grown in the full spectrum of daylight. Some plants, like soybeans, tomatoes, four-o'clocks, and coleus, attain a much greater final height under the absence of blue-violet radiation, but others, like sunflowers, buckwheat, Sudan grass, and other sun plants, do not. Soybeans become twiners under these conditions (Fig. 100, *B*). All plants, regardless of their final height, have much thinner stems, poorly differentiated internal tissues, poor development of flowers, fruits, and general storage organs, much lower fresh and dry weights, and a higher percentage of moisture than do plants grown in full sunlight. In general, they resemble plants grown in darkness (Figs. 99, 100). The same effects are produced when the region below $472\text{ m}\mu$ is eliminated but not to so marked an extent.

On the other hand, plants grown in the absence of the red end of the spectrum, even at greatly reduced intensity, develop more nearly like normal plants. The blue-violet end of the spectrum seems to be much more efficient in dry-weight production than the red end of the spectrum,

though not so efficient as the full spectrum. This is true in spite of the fact that the red end of the spectrum is more efficient in photosynthesis. The blue-violet end of the spectrum has a marked formative effect on the plant. It is chiefly this part of the spectrum that is responsible for the stunting effect of light on growth.

Plants grown in the absence of the ultraviolet portion of sunlight are little different from those grown in the full spectrum. This may be caused by the relatively low percentage of ultraviolet (usually less than 1 per cent of the total radiation) present in sunlight at comparatively low altitudes. At higher altitudes, it has been thought that ultraviolet radiation may exert a strong formative effect on the plant which may partly account for the reduced stature of plants in alpine regions. When a source of radiation rich in ultraviolet of shorter wave lengths than those found in sunlight is used, plants are seriously injured and often killed by it.

Infrared radiation of high intensity may also injure plants through the rise in temperature that it causes by being absorbed by the plant. The ordinary infrared of sunlight acts like darkness in its effect on growth. X rays in moderate doses have been reported to be injurious to many kinds of plants. X rays are much more penetrative than ultraviolet radiation and therefore are capable of more deep-seated effects on the plant. In general, they check growth and cause abnormalities in the structure of the plant. In a few instances, extremely light doses of X rays have been reported to stimulate the growth of some plants. X rays are not present in the ordinary radiation to which plants are exposed.

Effects of Duration of Radiation—Photoperiodism. In temperate regions, plants growing in nature are subjected to alternations of light and darkness. Day lengths range from 15 hr. in summer to about 9 hr. in winter. It has been found that the growth of plants and particularly the development of flowers and fruits is markedly influenced by the length of day. This response of plants to length of the daily period of illumination has been called **photoperiodism**.

Normally, the plant can attain the flowering stage only when the length of day falls within certain limits. These limits are reached only at certain seasons of the year. Some plants like radish and lettuce bloom only during long days (12 hr. or more) (Fig. 101, *B*). Such plants are called **long-day plants** and bloom normally in midsummer. Others, called **short-day plants**, require a short day (less than 12 hr.) for flowering and bloom normally either late in autumn or early in the spring. Examples of short-day plants are most of the spring flowers and such autumn-flowering plants as ragweeds, asters, cosmos, and scarlet sage (*Salvia splendens*) (Fig. 101, *A*). Still other plants, like the tomato, respond to all day lengths and therefore may bloom all year round.

When short-day plants are kept under long-day conditions, they usually

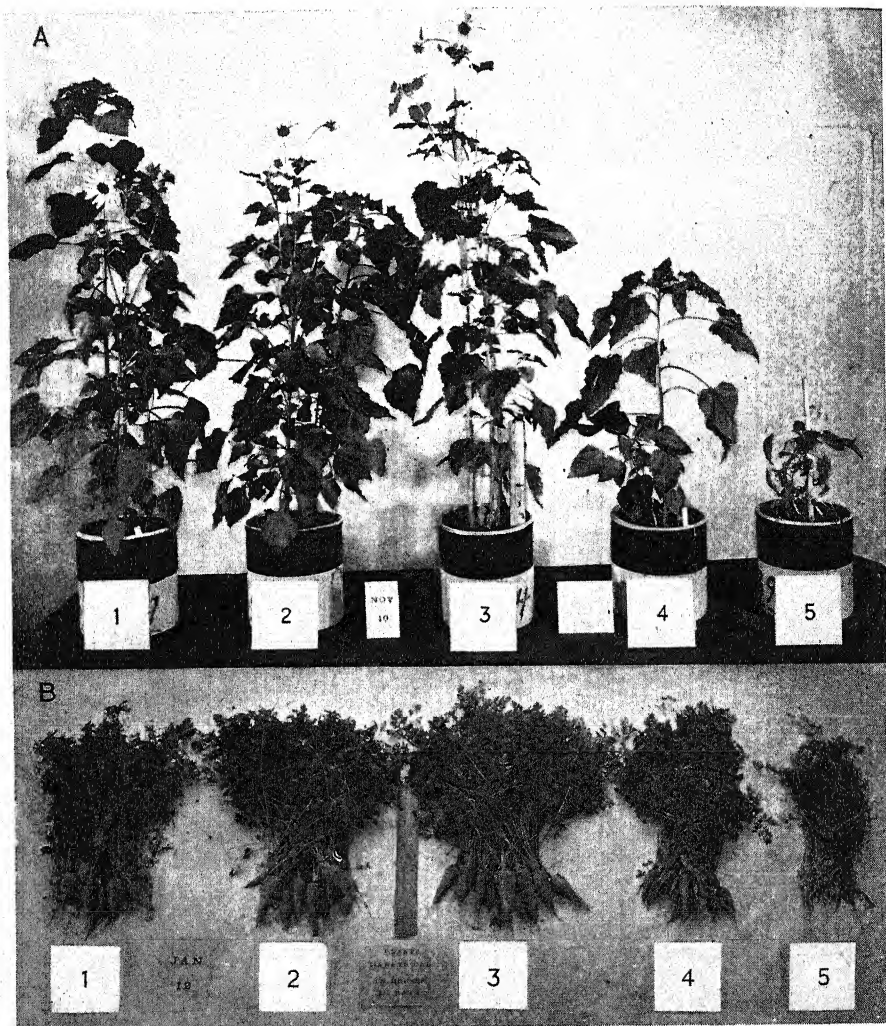


FIG. 99. Effect of quality of radiation on plant growth. *A*, sunflower plants, eighty days old; *B*, carrots, one hundred forty-three days old. 1, grown under ordinary greenhouse glass transmitting down to 312 $m\mu$; 2, grown under a clear glass transmitting down to 296 $m\mu$; 3, grown under a light-yellow glass which eliminated practically all ultraviolet radiation, transmitting down to 389 $m\mu$; 4, grown under a yellow glass which eliminated all violet and ultraviolet and part of the blue, transmitting down to 472 $m\mu$; 5, grown under an orange glass which eliminated all ultraviolet, violet, blue, and half of the green, transmitting chiefly red, orange, and yellow, lower limit 529 $m\mu$. (From H. W. Popp, *A Physiological Study of the Effect of Various Ranges of Wave Length on the Growth of Plants*, *Amer. Jour. Botany*, **13**: 706-736, 1926.)

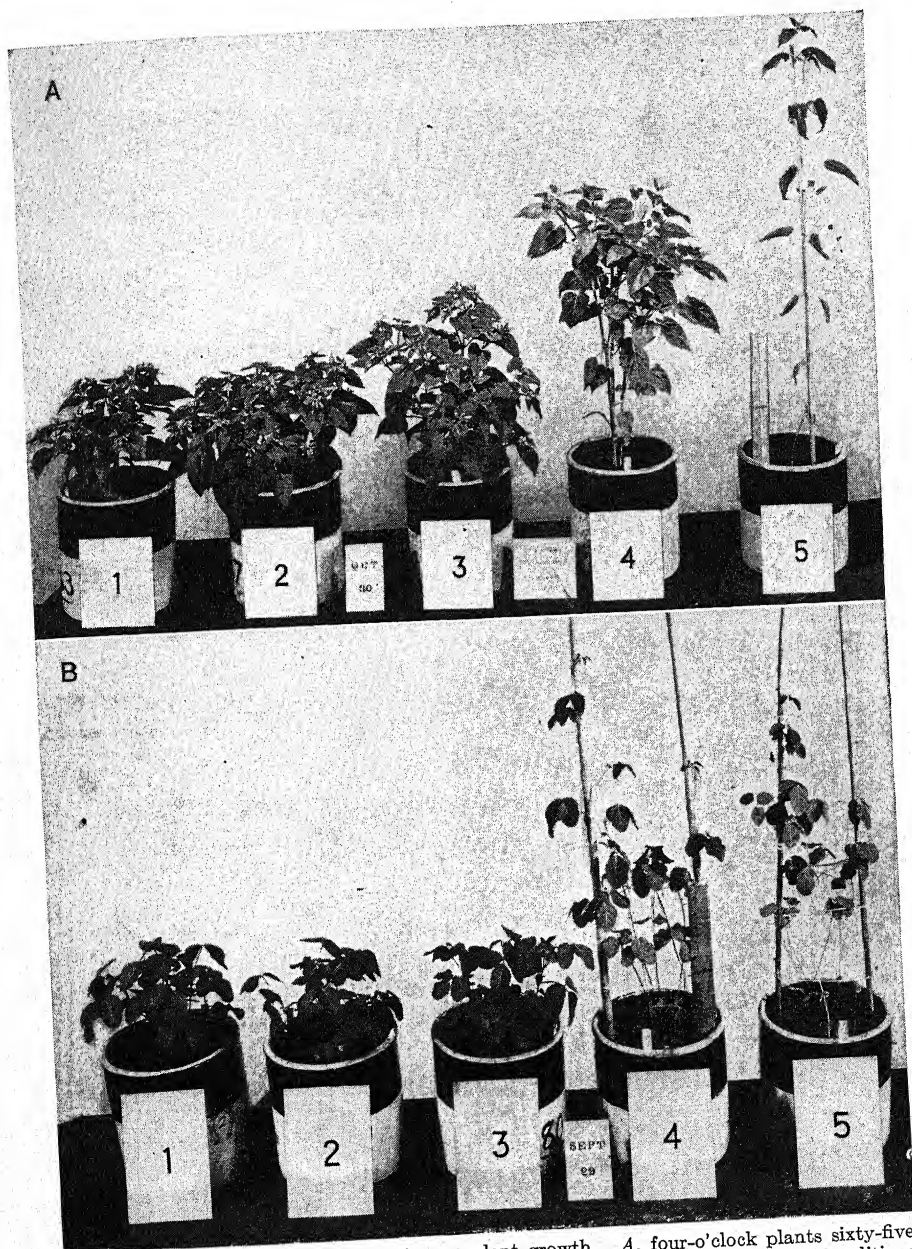


FIG. 100. Effect of quality of radiation on plant growth. A, four-o'clock plants sixty-five days old; B, Peking soybean plants, thirty-four days old. Numbers refer to same conditions as in Fig. 99. Note that the elimination of only ultraviolet radiation (3) has little effect on the growth of the plants, while elimination of the visible blue and violet along with the ultraviolet (4 and 5) causes marked changes in growth and development, the soybeans becoming twiners. (From H. W. Popp, *A Physiological Study of the Effect of Various Ranges of Wave Length on the Growth of Plants*, *Amer. Jour. Botany*, 13: 706-736, 1926.)

continue to grow vegetatively without flowering and may reach an unusual size. Many long-day plants when kept under a short day grow weakly vegetatively but fail to flower. Long-day herbaceous perennials like some

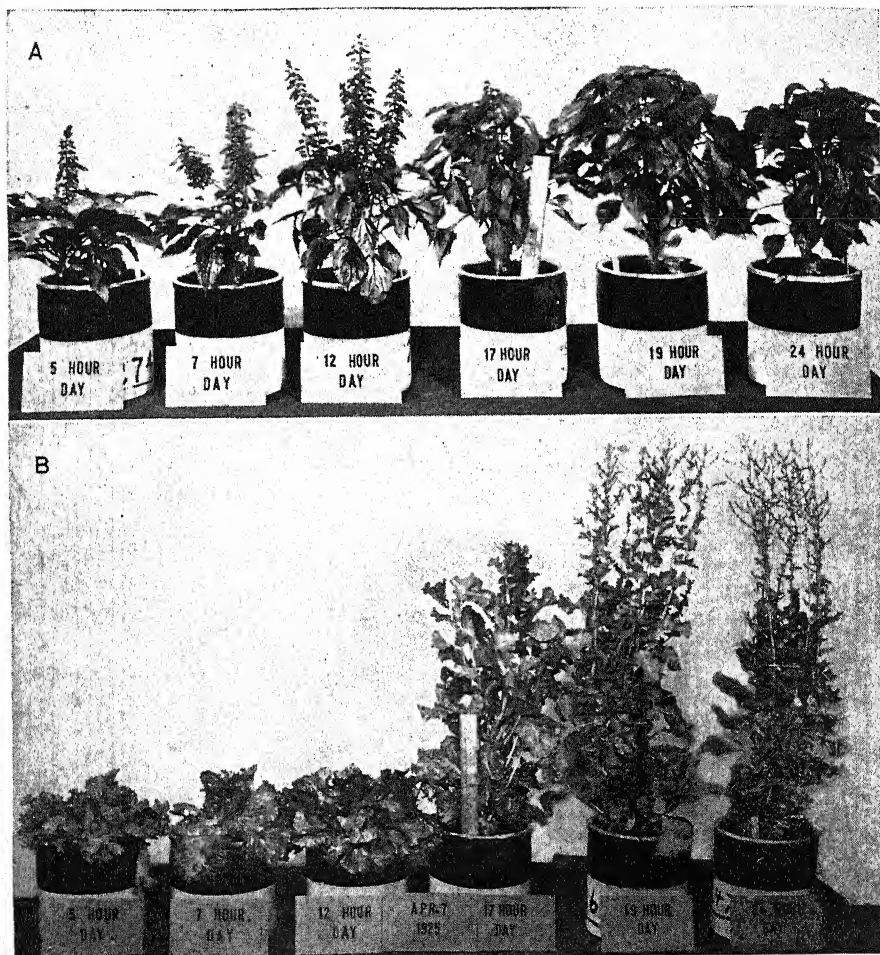


FIG. 101. Effect of length of day on plants. A, scarlet sage (*Salvia splendens*), a short-day plant; B, lettuce, a long-day plant. The day lengths to which the plants were subjected are indicated on the pots. (Photographs furnished by Dr. John M. Arthur, Boyce Thompson Institute For Plant Research, Inc., Yonkers, N.Y.)

of the sedums have been kept for 8 to 9 years under a short day without flowering, while controls receiving normal day lengths flowered every year during this time. One of these plants after having been kept under a short day for 8 years was given the full day length of summer and bloomed nor-

mally at the same time as did the control plants. In all types, the amount of vegetative growth is greatest under a long day. While many plants are on the border line between short-day and long-day plants, they probably have an optimum day length for flowering.

A day that is lengthened by means of artificial light, even of low intensity, seems to be as effective as the normal long day of midsummer in bringing long-day plants into flower. By this means it is possible to hasten the flowering of greenhouse long-day plants or to check the flowering of short-day plants. On the other hand, while the long days of midsummer may be shortened by not placing the plants in light so early in the morning or placing them in the dark in the afternoon, midday darkening does not produce the effect of a short day. Thus it has been reported that short-day plants placed in the dark between 10:00 A.M. and 3:00 P.M. in midsummer failed to flower or, in other words, responded as though they had been subjected to full summer light.

When plants receive alternations of light and darkness of 6 hr. or less, they respond as though kept under a long day or under continuous illumination. When given 10 hr. of light every other day or a full day (15 hr.) of light every other day in midsummer, plants respond as though kept under short-day conditions.

Length of day has also been reported to have an influence on the formation of tubers and bulbs, the character and extent of branching, root growth, abscission and leaf fall, dormancy and rejuvenescence, and the habits of annuals, biennials, and perennials.

Plants have also been raised from seed to seed in continuous artificial light. In nature, plants are not subjected to continuous illumination except in polar and subpolar regions. Some plants are apparently able to grow normally in continuous light while others are not. Tomatoes are injured and finally killed in any day length over 19 hr. Many short-day plants fail to flower under continuous illumination.

TEMPERATURE

As previously stated, growth of the plant proceeds as a result of constructive metabolism. New materials are constantly being synthesized and others broken down in the building of protoplasm. This involves a series of complex chemical reactions, all of which are influenced by temperature. Temperature determines the rate at which these processes take place and since the rate of growth is determined by the rate of these processes, temperature likewise affects the rate of growth. As will be seen later, it also exerts an important formative effect on the plant.

Temperature Range and Life Duration. The range of temperatures within which plants can live and grow varies with the species, with the

different parts of the same plant, and with the general external and internal conditions to which the plant has been subjected either before or during the application of a change in temperature. It varies particularly with the condition of the protoplasm.

As a rule, plants do not thrive when moved much more than a hundred miles north or south of the region to which they are indigenous, largely because of the difference in prevailing temperatures in different latitudes. Thus tropical plants usually fail to thrive in temperate regions, nor can most plants of temperate regions be made to grow in the tropics except at high altitudes. In high mountainous regions of the tropics, there is often the same range of plant associations extending from the lowland regions to the tops of the mountains as is found in going from the tropics toward the polar regions. Temperature is thus one of the most important factors determining the distribution of plants over the earth's surface.

In general, resting organs like seeds and spores can withstand a much wider range of temperatures than can growing plants. Cases have been reported of seeds that were able to germinate after having been subjected for a short time to a temperature as low as -180°C . or as high as 103°C . Seeds taken by the Greely expedition in 1883 to Fort Conger, about 490 miles from the North Pole, were found in 1899 by the Peary party and sent to the United States, where they remained unplanted until the spring of 1905. At this time, lettuce and radish seeds from the lot were planted. The lettuce failed to grow but about half of the radish seeds germinated and produced vigorous plants that produced seed. The ability of bacterial spores to withstand extreme temperatures is well known. Many spores can be boiled or frozen without injuring them. Resting organs like some tubers, bulbs, and the branches of deciduous trees in winter are also able to withstand wide ranges of temperature without injury. Succulent plants usually have a much narrower range within which they can live and grow.

The ability of growing plants to withstand low or high temperatures is governed by the conditions to which the plants are subjected. A sudden change in temperature is more likely to prove injurious than a gradual change. Many plants, when gradually subjected to lower and lower or higher and higher temperatures are able to adapt themselves to it. Such adaptation involves fundamental changes in the condition of the protoplasm and particularly its degree of hydration. The ratio of bound water to free water is usually higher in resistant plant organs. Thus seeds that have imbibed water and swollen are much less resistant to extremes of temperature than are dry seeds in which much of the moisture present is bound water. More will be said later concerning bound water in connection with the discussion of subminimal temperatures. In addition to the water relations, many other factors, including age, the presence of

osmotically active substances, and the general structure of the plant, play a part in determining the range of temperatures within which the plant can continue to live.

Cardinal Points of Temperature for Growth. The range of temperatures within which plants are able to grow may be designated by three cardinal points, *viz.*, the **minimum**, or temperature below which no growth takes place, the **optimum**, which is usually considered the temperature which gives the highest rate of growth or is the best for growth, and the **maximum** temperature, above which no growth takes place. These cardinal points are not fixed during the life of the plant, nor are they always the same for all parts of the plant. The cardinal points for root growth may be different from those for stem growth. Those for flower development are frequently different from those for vegetative growth. This is clearly shown in many plants that flower very early in spring before the vegetative shoots have developed. Seeds will sometimes germinate at much lower temperatures than the more mature plants need for growth. Although many variations occur among different species, the minimum temperature for growth of temperate plants is usually somewhat above the freezing point of water and the maximum around 45 to 50°C. The optimum usually averages around 30°C.

The optimum temperature for growth is conditioned by the length of time the plant is kept under the influence of this temperature. For example, plants may grow most rapidly for a short period of time at 35°C.; but if this temperature is maintained, the rate may decrease below the rate obtained under a constant temperature that is lower. For this reason a fourth cardinal point is sometimes recognized which has been called the **maximum-rate** temperature and denotes the temperature at which the rate of growth reaches its highest intensity, though only for a short time. The true optimum temperature would then be the temperature at which growth proceeds most rapidly regardless of how long this temperature is maintained. In other words, the plant is able to maintain its most rapid growth indefinitely until maturity at the true optimum temperature.

In general, the rate of growth of a plant is lowest near the minimum, gradually increases as the temperature rises toward the optimum, and falls off again toward the maximum. The optimum temperature is not always midway between the minimum and maximum but more often lies nearer the maximum than the minimum.

Supramaximal Temperatures. When plants are subjected to temperatures above the maximum, *i.e.*, supramaximal temperatures, they are sooner or later killed, the time required depending upon how much above the maximum the temperature is. Ordinary plants are killed in

1 to $1\frac{1}{2}$ hr. when the temperature is 1 to $1\frac{1}{2}^{\circ}$ above the maximum. When the temperature is very much above the maximum, death may be almost instantaneous. Every $10^{\circ}\text{C}.$ rise above the maximum shortens the time required to cause death from ten to one hundred fifty times. From the fact that this relationship of temperature also holds in the coagulation of many proteins, it has been thought that death of plants under high temperatures may be caused by the coagulation or gelation of the protoplasm. A condition develops in the cells which is referred to as **heat rigor**. The protoplasm becomes set and a return to normal is impossible.

Subminimal Temperatures. Temperatures below the minimum also cause death if prolonged. In this case, a **cold rigor** develops and the protoplasm becomes set as it does in heat rigor. This condition develops in thermophilic fungi and bacteria at ordinary temperatures, these plants having a high minimum temperature. Some tropical plants are likewise killed at temperatures above the freezing point, which indicates that freezing is not necessary to cause death. With many temperate plants, however, freezing is a common cause of injury and death. This is readily observed after the first heavy frost in autumn when many garden plants, previously green and vigorous, wilt, turn brown, and die. Some plants, however, and especially perennials are able to withstand severe freezing.

When death is caused at temperatures slightly above $0^{\circ}\text{C}.$, it may result from wilting or from disturbed metabolism. When plants like tobacco, pumpkin, or beans have been growing under ordinary temperatures and are suddenly transferred to an air temperature of 2 to $4^{\circ}\text{C}.$, they wilt. If the temperature of the soil in which these plants are growing is raised to $18^{\circ}\text{C}.$ without raising the air temperature above 2 to $4^{\circ}\text{C}.$, they do not wilt. In this case, it is evident that wilting results from a more rapid loss of water by transpiration than can be supplied by absorption at the low temperature or, in other words, at low temperatures absorption is reduced more than water loss, and the plant wilts. Many greenhouse plants like coleus, however, are killed by temperatures slightly above freezing before wilting occurs. In such plants, the leaves usually become spotted when the temperature is too low, and these spots increase in size until finally the leaves turn brown and die. This happens in about four days at $3^{\circ}\text{C}.$ In plants of this kind, death is probably caused by disturbed metabolism.

Death resulting from actual freezing is much more common. There is a wide variation in plants in their ability to withstand freezing. Some can remain frozen all winter without being injured. In northern Siberia, forest trees are not killed even though the temperature may fall to -62 to $-64^{\circ}\text{C}.$ In north temperate regions, wheat, planted in autumn, is able

to survive severe winter weather. On the other hand, most annuals and many other plants are killed by freezing temperatures.

Since plants always contain salts in solution, the actual freezing point is usually several degrees below the freezing point of water. When freezing does occur, ice usually forms first in the intercellular spaces. If freezing is severe, ice may also form within the cells and the whole tissue become frozen solid. The formation of ice in the intercellular spaces results in the removal of water from the cells. This removal of water is one of the most common causes of death, since it leads to coagulation and irreversible precipitation of the cell colloids. The increased concentration of salts under these conditions also contributes to this precipitation. Since water expands on freezing, there is also often a tearing or rupture of the cells resulting from it.

Hardening. The ability of plants to withstand freezing depends upon their general structure as well as upon the condition of the protoplasm. Both of these in turn depend partly upon the conditions under which the plants have been grown. Plants with a thick epidermis and compact internal tissues are sometimes more resistant to freezing than are those loosely constructed. The resistance to freezing also increases with increased concentration of the cell sap and particularly with the ability of the tissues to bind water. These conditions can be developed in some plants by gradually subjecting them to lower and lower temperatures or, in other words, by **hardening** them. The gardener usually hardens his vegetables, before he transfers them to the open in spring, by first keeping them for a time in a cold frame. In nature, hardening naturally occurs in many plants during autumn and early winter. Some plants cannot be hardened in this manner. Such plants are easily killed by freezing temperatures. In species that are winter hardy, it has been found that hydrophilic colloids develop during the process of hardening, which enable these plants to bind water so that it cannot readily freeze. Winter-hardy varieties of wheat, for example, are those which develop a relatively high percentage of bound water as the temperature is gradually reduced. Such plants also have a more compact structure and other features that enable them to withstand freezing. These conditions do not develop, however, even in winter-hardy plants unless the temperature has been gradually lowered. Winter-hardy plants as well as susceptible varieties, if first grown in a greenhouse and then suddenly subjected to freezing temperatures, are immediately killed.

Formative Effects of Temperature. Temperature has a marked influence on the size, form, and general structure of the plant. These formative effects appear most striking when the temperature is near the

minimum or near the maximum for growth. When plants are kept constantly under low temperatures, the length of the growing zone increases but the internodes remain short, resulting in a plant of comparatively low stature. On the other hand, when they are kept under high temperatures, the length of the growing zone decreases, the internodes become longer and the plants become taller. Some plants develop a type of etiolation at high temperatures. This is true of potatoes. Potatoes develop tubers best at low to medium temperatures and hence can be grown more successfully in northern temperate regions like Maine. A European variety of potatoes has been reported to produce only tubers and no vegetative shoots when grown at a temperature of 6 to 7°C. Many plants develop excessive vegetative growth at high temperatures. Under these conditions there is probably a rapid rate of respiration and other metabolic changes that tend to deplete carbohydrates to such an extent that they do not accumulate and hence storage organs are poorly developed.

Temperature also affects flowering and fruiting. The temperature under which seeds are germinated may affect the later growth of the plant. In many other ways, temperature is important in the growth of the plant. It should, however, be mentioned that temperature always operates through the change that it induces in the internal conditions of the plant.

MOISTURE

The importance of water to the plant has been emphasized in Chap. 7. The loss of water by transpiration has also been considered in Chap. 4. These matters will not be considered further here. Growth takes place only in turgid cells, and this necessitates an ample supply of water. The amount of available water, like radiation and temperature, may influence to a marked degree the form, structure, and nature of growth of plants. The cardinal points of moisture have not been so accurately determined, but excessive moisture or excessive dryness are both likely to be unfavorable to the growth of most plants. Only plants with some degree of plasticity are able to adjust themselves to radical changes in moisture conditions. Those lacking such plasticity are often killed by drought or by a waterlogged soil. The conditions of the plant that enable them to withstand drought have already been mentioned in connection with transpiration (Chap. 4).

In general, herbaceous plants growing under conditions of high moisture tend to have loose, succulent tissues with numerous air spaces. Strengthening tissues are often poorly developed and cuticular and suberized membranes are reduced or entirely absent. Many plants fail to develop root hairs when the roots are in water. In very humid regions, the stems of plants are likely to be more elongated and the leaves broader and

thinner. Many of these features develop also under conditions of low light intensity. Since plants in shaded places are subjected both to lower light intensity and to higher humidity, it is not always possible to separate the effects of one from the other. Plants that have developed under conditions of this type are usually killed in a short time when subjected to a dry atmosphere. Plants that are capable of living both upon land and in water often assume an entirely different form on land from that which they have in water. Submersed leaves of such plants are often finely dissected. The internal structures are also decidedly different.

In contrast to plants of very humid habitats, those growing under very dry situations tend to be small of stature and compact in form. The stems are short and stout and the leaves small and thick. Often the leaves are mere scales or spines. Epidermal layers are heavily cutinized and sometimes covered with bloom or hairs. Stomata are few in number and in some species are sunken below the level of the epidermis. Such plants may also have a higher concentration of cell sap and therefore higher osmotic pressures within the cells. Hydrophilic colloids are often present in abundance and enable such plants to bind and hold such water as is available to them. Many of the features mentioned are also developed under high light intensity. Light and dryness probably both contribute toward causing such formative effects, since they are often both operative in the same locality.

A plant may have its roots in water and still develop as though it were grown in a dry situation. The stems and leaves of many swamp and bog plants resemble those of plants grown in arid regions. This may be explained by the fact that such plants may have difficulty in absorbing water because of the high osmotic pressure or the unfavorable acidity of the external medium or for some other reason. Situations of this kind are considered physiologically dry. Plants growing in salt marshes usually have high osmotic pressures. Some of the highest values of osmotic pressure that have been recorded in plants were found in plants growing along the edges of the Great Salt Lake. A situation which promotes excessive transpiration, even though there may be an abundance of water in the soil, may also be considered a physiologically dry one.

According to the abundance of available water in the habitats in which they naturally grow, plants may be classified as **hydrophytes**, those which grow directly in water or in very wet places; **mesophytes**, those found in ordinary humid regions with a moderate, though ample supply of water; and **xerophytes**, those growing in very dry or desert regions where conditions are conducive to excessive transpiration. A fourth group, **halophytes**, is sometimes added, which includes plants growing in salt marshes where the concentration of the soil solution is so high as to make absorption of water difficult. Halophytes are in reality xerophytes.

PLANT MOVEMENTS

Since the plants with which we are most familiar are rooted in the ground and hence do not move from place to place, the capacity of movement is often thought to be entirely lacking in plants. However, among the simpler forms there are entire plants which move from place to place, and the parts or organs of stationary plants may change their positions. Thus flower petals open and close and roots and stems may change their direction of growth and bend or curve under certain conditions. Ordinarily, however, the rate of movement is not rapid enough for observation except with the aid of some special device. Motion-picture films, requiring hours or days for exposure but projected in a period of a few minutes, give striking demonstrations of many plant movements, such as the opening of flowers and the nodding of stems.

Growth Movements and Turgor Movements. Many plant movements are growth movements. Increase in size in itself involves movement, since the expanding organ occupies more and more space. Growth movements may also be caused by a change in either the rate or direction of growth. Thus, in a stem tip bending toward the light in response to one-sided illumination, the convex side is growing more rapidly than the concave side. In flower buds opening in response to an increase of temperature, the upper (inner) surface of the petals grows more rapidly than the lower surface, causing the petals to open outward. Such movements can occur only in the growing regions of plants and hence are termed **growth movements**.

Movements may also occur in mature organs and in such cases are usually not growth movements. Often these movements are the result of changes in the turgor pressure of certain cells, which in turn is thought to be caused by changes in the permeability of these cells. Turgor movements are usually more rapid than growth movements and may occur over and over again in the same organ. For this reason, they are sometimes called **movements of variation** or movements of alternation, in contrast to growth movements. The reaction of the sensitive plant (*Mimosa pudica*) (Fig. 103, A, B) to the touch is a well-known example of a turgor movement. The opening and closing of stomata caused by changes in the turgor pressure of the guard cells are also movements of variation.

Autonomic Movements and Paratonic Movements. Growth such as the elongation of a stem or a root may be regarded as a slow movement performed by the growing organ. Such movements, occurring spontaneously because of activities going on within the plant and not directly related to any change in the environment, are called **autonomic movements**. Since the rate of elongation on all sides of a stem tip is not uni-

form, even under apparently constant environmental conditions, the movement of the stem tip as it elongates rarely occurs in the direction of a straight line. Instead, because of this unequal growth in different sections around the stem, the stem apex bends or nods from one side to another as it elongates, and the direction of growth is a loose spiral. This bending or nodding is an autonomic growth movement known as **nutatation** or **circumnutation**.

Paratonic or stimulus movements, in contrast to autonomic movements, are caused by changes in the environment known as **stimuli**. Stimuli may be mechanical, chemical, or ethereal and include such agents as the force of gravity, contact, oxygen, water, acids, alkalies, salts, other chemicals, heat, light, and electricity. Plants move or respond to these stimuli because of one of the fundamental properties of protoplasm termed **irritability**. Irritability may be defined as the sensitiveness of protoplasm or its capacity to respond to the influence of stimuli. The minimum length of time necessary for a stimulus to act upon a plant in order to bring about a later response is called the **presentation period**, and the period of time which elapses from the initiation of the stimulus until the visible beginning of the reaction is called the **reaction time**. The reaction or response of a plant to a stimulus may not begin until some time after the stimulus is applied and may continue after the stimulus is removed.

Types of Paratonic, or Stimulus, Movements—Nasties. Paratonic movements of such a nature that the direction of movement is independent of the direction from which the stimulus is applied are called **nasties**. Nasties are responses of bilaterally symmetrical organs like leaves and flower petals, and the direction of movement is largely determined by the anatomy or structure of the organ. They occur more commonly in mature plant organs than in growing parts and hence in many cases are movements of variation or alternation rather than growth movements.

Nasties caused by changes in light intensity are called **photonasties**. For example, many flowers open under intense illumination and close in the dark or under weak illumination. The common dandelion opens on bright days but closes not only at night but on dull days or if artificially shaded. On the other hand, some flowers, like those of four-o'clocks or tobacco, open in light of low intensity and close under intense illumination.

Nasties caused by changes in temperature are called **thermonasties**. The rapid opening of certain flowers when brought into a warm room from a cold place is a thermonasty brought about by the increased rate of elongation of the upper side of the petals over that of the lower side.

Certain leaves as well as flowers may fold up at night. These so-called

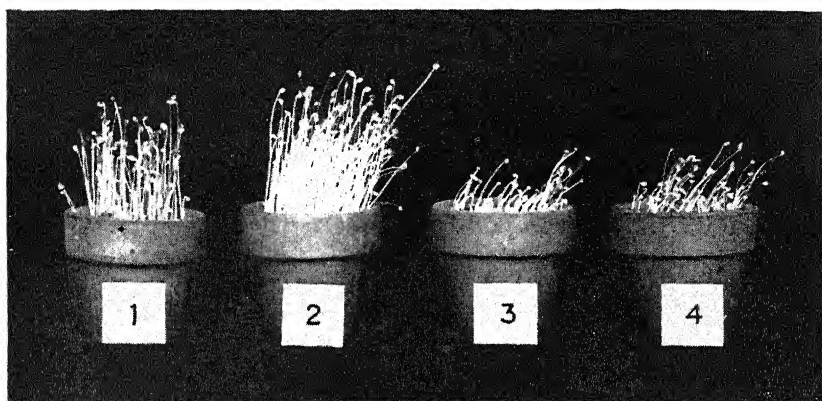


FIG. 102. Phototropism; effect of different colors of light. Turnip seedlings subjected to one-sided illumination from right; 1, to red light; 2, to green light; 3, to blue light; and 4, to white light (sunlight).

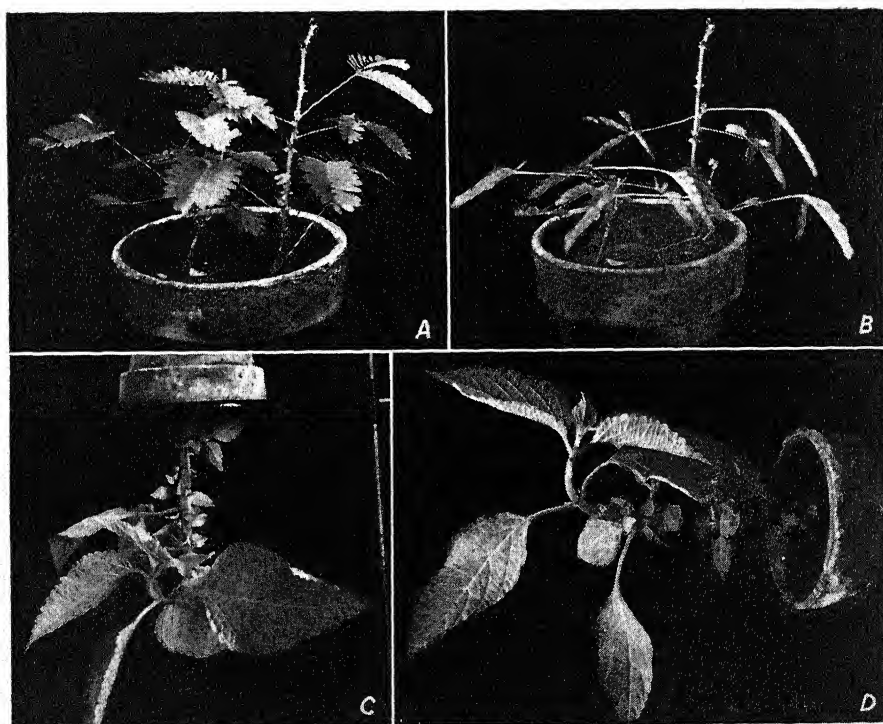


FIG. 103. A-B, sensitive plant (*Mimosa pudica*). A, undisturbed plant; B, the same plant after the stem had been shaken; note that the leaves droop and the leaflets fold together as a result of the shock stimulus; C-D, geotropism as shown by stem of *Coleus*; C, curvature 24 hr. after plant had been suspended vertically downward; D, curvature of stem 24-hr. after plant had been placed in a horizontal position.

"sleep movements" of plants, brought about by the alternation of night and day, are the most common nastics and are termed **nyctinasties**. They are, of course, in no way related to the sleep of animals but are caused by changes in temperature or light intensity or both.

One of the most prominent and best known of the nastic turgor movements is furnished by the sensitive plant (*Mimosa pudica*), which rapidly droops its leaves when touched (Fig. 103, A, B). In addition, the leaflets fold in pairs. A very strong irritation of one leaf may be transmitted throughout the plant, the leaflets folding and the leaflets drooping one after another. This type of movement is very unusual in plants.

Taxies and Tropisms. Paratonic or stimulus movements of such a nature that the direction of movement is determined by the direction of the stimulus, *i.e.*, movements caused by unilateral stimulation, may

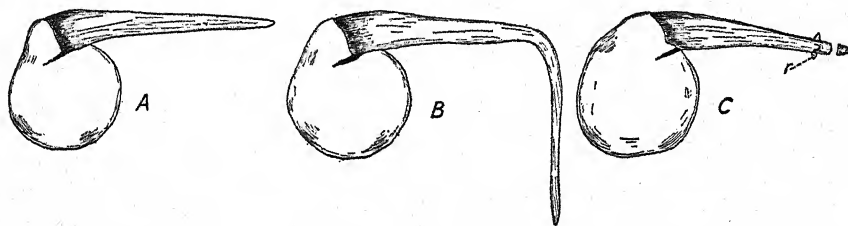


FIG. 104. Geotropism as shown by roots of peas. A, seedling of pea with root placed horizontally; B, the same root, 24 hr. later, the growing tip having bent down in response to gravity; C, a seedling with 4 mm. of tip removed and then placed horizontally; note that, when the growing tip is removed, the root fails to respond to the stimulus; secondary roots have started to develop at *r*. Compare with Fig. 46, in which roots have been placed vertically. (Drawn by F. Brown.)

be either **taxies** or **tropisms**. Certain unicellular algae, some bacteria, and certain reproductive cells of higher plants are provided with cilia or flagella and exhibit free locomotion of the entire body in response to and determined by the direction of stimuli such as light, temperature, or chemical constitution of the environment. These movements are called **taxies**.

Tropisms are typically responses of radially symmetrical organs, like roots and stems, and of the growing parts of these. Hence they are typically growth movements. Depending upon the nature of the stimulus a tropism may be called **phototropism**, **geotropism**, **hydrotropism**, etc. The capacity of turning toward or away from light is known as **phototropism**. (When sunlight is the stimulus, the movement is sometimes called **heliotropism**.) Young growing stems usually bend toward the light (Fig. 102) and thus exhibit positive phototropism. It is chiefly the blue end of the spectrum that is responsible for the movement. Under-

ground stems and roots are often indifferent to light, but some roots, such as those of mustard, bend away from the light and thus exhibit negative phototropism. Largely because of phototropic movements, the leaves of many plants form a so-called **leaf mosaic** (Fig. 22) in which the leaf blades are so situated that they rarely shade each other but fill in all spaces so that a solid pattern of leaf blades presents itself in a direction perpendicular to that of the light rays falling on them.

The capacity of roots and stems to orient themselves with regard to the force of gravity is called **geotropism**. Taproots, if directed in any way except vertically downward, generally turn downward and exhibit positive geotropism (Fig. 104). The greatest curvature is always in the region of greatest elongation. The fully grown parts do not bend. Similarly, stems which normally grow vertically upward will if moved into any other position bend upward and exhibit negative geotropism (Fig. 103, C, D). There are numerous other stimuli which may cause tropisms in growing organs.

The positive phototropism and negative geotropism of stems can be explained by differences in auxin activity on opposite sides of the stem under unilateral stimulation. Light, and especially short-wave-length radiation, seems to check auxin activity. Thus, when a stem is exposed to one-sided illumination, the auxin activity is greater on the side away from the light, causing that side to grow more rapidly. This causes the stem to bend toward light. Similarly, when a stem is placed horizontally, auxin seems to accumulate on the lower side, causing that side to grow more rapidly. The stem, therefore, bends upward or is negatively geotropic. Root growth is thought to be stimulated by much lower concentrations of auxin and to be inhibited by concentrations that stimulate stem growth. Thus, when roots are placed horizontally, auxin again accumulates on the lower side but this inhibits the growth on that side, causing the root to grow more on the opposite side. Roots therefore bend downward, or are positively geotropic. For the same reason, many of them are negatively phototropic.

Hygroscopic movements, such as the twisting of awns of certain species of wild oats or the movement of the elaters of liverwort sporophytes, cannot properly be called stimulus movements since they are purely physical phenomena and not related to the irritability of protoplasm. They are usually caused by imbibition and loss of water.

CHAPTER 10

FLOWERS

Attention has been given in previous chapters to the structure and functions of the vegetative parts of plants, *i.e.*, to roots, stems, and leaves. Except as these organs function secondarily in vegetative propagation, the reproductive processes of plants have not been discussed. The flower is the structure concerned in the sexual reproductive processes of higher plants. Flowers lead to the production of fruits and seeds.

GENERAL STRUCTURE OF FLOWERS

Parts of the Flower. Flowers may be composed of as many as four different sets of parts. These are, enumerated in order from outside to center of the flower, **sepals**, **petals**, **stamens**, and **pistils** (Fig. 105, A). The stem apex to which these are attached is known as the **receptacle**. The sepals collectively constitute the **calyx**, and the petals the **corolla**. The stamens collectively constitute the **androecium**, and the pistil or pistils collectively are called the **gynoecium**. These four sets of parts may be attached at different levels on a somewhat elongated receptacle, or they may be attached in more or less concentric rings or whorls on a flattened receptacle. In some flowers, this arrangement is obscured, and the petals may seem to arise from the sepals, and the stamens from the corolla. Sepals and pistils can usually be seen attached to the receptacle.

When a flower has all four sets of parts, it is said to be **complete**. In many flowers, one or more of the sets may be lacking. If any one of the four sets of parts is lacking, the flower is **incomplete**. Stamens and pistils are regarded as the essential parts of the flower. Both must be present, either in the same or in different flowers, in order to have sexual reproduction and the resultant formation of seed. If the flower lacks either stamens or pistils it is said to be **imperfect**. When both stamens and pistils are present, the flower is said to be **perfect** regardless of whether or not sepals or petals are present. Therefore, all complete flowers are perfect; incomplete flowers may be either perfect or imperfect, depending upon whether or not both stamens and pistils are present. Imperfect flowers are of two types; those bearing pistils but not stamens (**pistillate flowers**) (Fig. 108, B), and those bearing stamens but not pistils (**staminate flowers**) (Fig. 108, A). When both these types of flowers are produced on the same plant, the species of plant is said to be **monoecious**, a term meaning "one household."

When only staminate flowers are produced on one individual plant and only pistillate flowers on another plant of the same species, the species is said to be **dioecious** (two households). Examples of monoecious species are corn (tassels bearing staminate flowers, the ear bearing pistillate flowers), cattails, alders, birches, walnuts, and hickories. Asparagus, willows, and cottonwoods are examples of dioecious species. Occasionally, as in the marginal flowers of the sunflower head and in the cultivated hydrangea and the snowball bush, neither stamens nor pistils are present. Such flowers are said to be **sterile**.

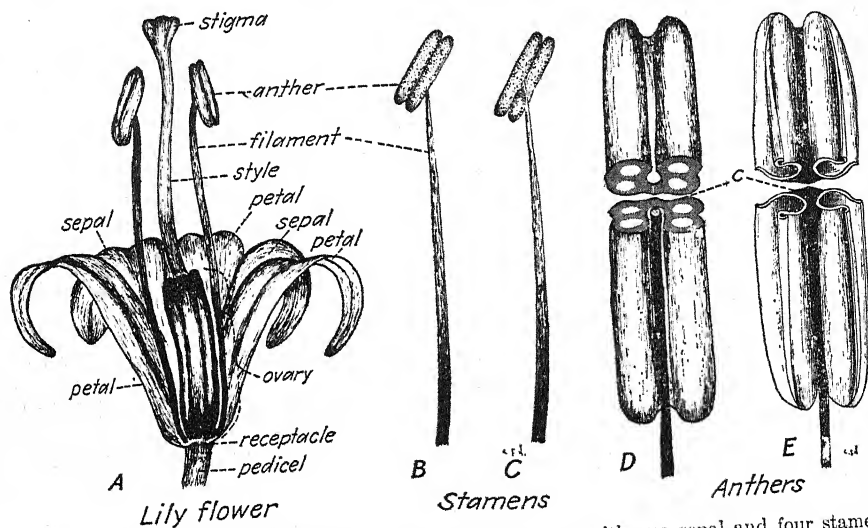


FIG. 105. Parts of the flower. A, drawing of flower of lily with one sepal and four stamens removed; B, front or external view of a stamen with versatile anther; C, view of stamen showing attachment of filament to anther; D, an immature anther cut in half showing the four pollen sacs and the connective, c; E, an anther after discharge of the pollen through the two lateral, longitudinal slits. (B, C, and E by Chris. Hildebrandt.)

Sepals and Petals. Sepals and petals together constitute the **perianth**. The perianth parts are frequently spoken of as **accessory** flower parts, *i.e.*, not essential to seed formation. Both may be lacking; but if only one set is lacking, the one present is always designated as the calyx. Typically, sepals are green and leaf-like; petals are often highly colored; occasionally, both are colored and nearly equal in size, as in tulips and lilies (Fig. 105, A). The number of sepals and petals is usually constant for a species of plant. Flowers of monocotyledons usually have three sepals and three petals; those of dicotyledons often have four or five of each.

The odors of flowers are caused by essential oils and other chemical substances that are formed in special secreting cells, usually of the petals. If

nectar glands, secreting a sugary liquid, are present, they are often situated at the bases of the petals on their inner surfaces, but they may occur in other places. Flower colors usually result from the presence of anthocyanin or carotenoid pigments. Both colors and odors are usually assumed to be of importance in attracting insects that effect pollination, *i.e.*, the transfer of the pollen from the anther of a stamen to the stigma of a pistil.

Both calyx and corolla, but especially the former, are protective structures prior to expansion of the flower bud.

Stamens. The stamens commonly form one or more whorls between the corolla and the pistil or pistils. The number of stamens per flower is variable and may or may not bear a relation to the number of sepals or petals. A flower may contain only a single stamen; more often the number is larger and definite, ranging from three in some species to ten in others; in some cases they are numerous. Each stamen usually consists of a stalk of **filament** bearing at its apex an **anther** (Fig. 105, A-C). The filament may be very short or may be entirely lacking, but in most cases it is elongated. The anther may be attached firmly at its base to the filament (**basal attachment**) or near its center, loosely permitting a rocking motion (**versatile anther**) (Fig. 105, B, C), or in other ways.

Viewed externally, an anther usually consists of two elongated lobes united by a tissue extending from base to tip of the anther, called the **connective** (Fig. 105, D, E). Examination of a cross section of the anther (Fig. 105, D; 106, A) reveals that each of these lobes consists of two elongated cavities, or **pollen sacs**, containing **pollen grains**. The outer cell layer of the wall of each cavity is an epidermis. Just under the epidermis is a layer of larger cells traversed by irregular hygroscopic bands. This layer is called the **endothecium** and plays a prominent role in the final dehiscence (splitting open) of the anther. Next to it are usually several middle layers of cells which often flatten in the mature anther, and finally, next to the cavity itself, the remains of a nutritive tissue called the **tape-tum**. Where the walls of the two adjacent cavities meet, externally, the cells are specialized as **lip cells**. At maturity, the anther splits open at the lip cells. The tissue between the two cavities breaks down, the two cavities thus becoming one. The pollen is then released through a longitudinal slit on each side of the anther (Fig. 105, E). In some cases, however, the pollen is shed through terminal slits or pores as in *Solanum*; by openings in tubular prolongations of the pollen sacs as in *Vaccinium*; or by hinged valves as in *Sassafras* and *Berberis*. In wind-pollinated flowers, like many of the grasses, the filaments elongate considerably at maturity, causing the anthers to become exerted beyond the surrounding floral tissue.

Pistils. The pistils are the central members of perfect and of pistillate flowers. In its ordinary form a pistil consists of three parts (Fig. 106, B);

the enlarged basal region is the **ovary**, the apex is the **stigma**, and the part between ovary and stigma is the **style**. The ovary contains one or more **ovules**, which later become seeds. The pistil in its simplest form is commonly considered to be a specialized leaf on which ovules are produced, the leaf having been inrolled and its margins or edges united in such a way as to

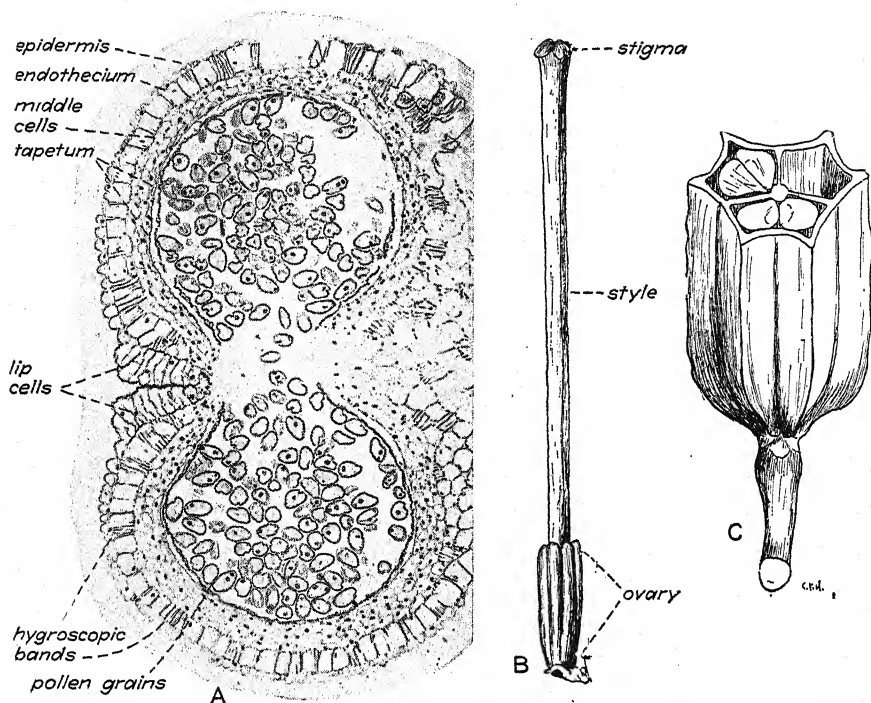


FIG. 106. A, photomicrograph of one-half of a lily anther when pollen grains are about ready to be discharged. The two cavities containing the pollen grains have become one through the breaking down of the tissue between them. Liberation of the pollen occurs through the separation of the lip cells. Note that some of the pollen grains show two nuclei. B, a compound pistil of lily enlarged showing parts. C, enlarged ovary of the lily, almost mature, cut crosswise to show the three ovarian segments each with a locule containing two rows of ovules. The ovules have been removed from one of the locules. (Drawings B and C by Chris. Hildebrandt.)

enclose the ovules completely. A single ovule-bearing leaf of this kind is called a **carpel**. If the pistil consists of only one such leaf (carpel), it is a **simple pistil**; if it is made up of two or more carpels, it is called a **compound pistil**. The flower of the common buttercup (*Ranunculus*) has simple pistils; lilies have a flower with a compound pistil consisting of three carpels.

In a compound pistil, the styles of the individual carpels may be separate throughout their length, or they may be united into a single **stylar column**.

Even in the latter case, there is likely to be an indication of the compound nature of the pistil in the number of lobes, or divisions, of the stigma.

The stigma receives pollen grains carried to it by various agencies. It is frequently provided with a sticky stigmatic fluid and it may be fitted with grooves or depressions or with tiny, stiff hairs or with glands, all of which facilitate the reception of pollen. The style is sometimes much elongated, elevating the stigma above the other floral parts. This also facilitates the interception of pollen grains. Sometimes the style is lacking, as in the tulip flower, in which case the stigma is sessile on the ovary.

A cross section of an ovary reveals one or more cavities, or **locules** (often called cells), in which the ovule or ovules are contained (Fig. 106, *C*). In general, each carpel has its own locule and thus there are usually as many locules in a compound pistil as there are carpels, the contiguous walls of the individual ovaries of the carpels often forming partitions in the ovary. In some cases, however, these partitions may not develop and thus the ovary may have only one cavity or locule even though the pistil is compound.

The portion of the ovary to which the ovules are attached is known as the **placenta**, and the manner in which the ovules are distributed in the ovary is called the **placentation**. The placentae usually occur on what might be considered the inrolled, united edges of the carpel. In a simple pistil, therefore, the ovules may occur in a double vertical row along one side of the ovary, or they may arise singly from the top, sides, or bottom of the ovary. The positions of the placentae in compound pistils vary with the structure of the ovary. When the placentae occur on the central axis of an ovary which has several locules, as in lily (Fig. 106, *C*; 107, *A*, *E*), the placentation is **axile**. In compound pistils in which there is only one cavity, or locule, the placentae may occur on the wall of the ovary, as in some species of *Drosera* and of *Ribes*, in which case it is called **parietal** placentation (Fig. 107, *F*), or there may be a central axis to which all ovules are attached. This is called **free central** placentation (Fig. 107, *G*, *H*) and occurs in pinks and in primroses.

The number of ovules contained in a single ovary varies from one, as in buckwheat flowers, to many hundreds, as in tobacco and poppy.

Form and Arrangement of Parts of the Flower. *Floral Symmetry.* In many flowers, like the lily (Fig. 105, *A*), the members of each whorl of parts are all alike and are arranged radially around a central axis. Such a flower is said to be **regular** or **actinomorphic** or to have **radial symmetry**. When a flower of this type is cut vertically in any plane through the center, the resulting halves are somewhat like mirror images of each other. In other flowers, such as sweet peas, snapdragons (Fig. 108, *G*), and violets, one or more of the petals, and frequently of the sepals and stamens also, are unlike the others in shape or form. Such a flower can be cut in only

one vertical plane to obtain halves that are like mirror images of each other. The flower is then **irregular**, or **zygomorphic**, and has **bilateral symmetry**. Less often some of the sets of parts of a flower are spirally arranged. Thus in buttercups (Fig. 309, *B*, *C*) the stamens and pistils are spirally arranged

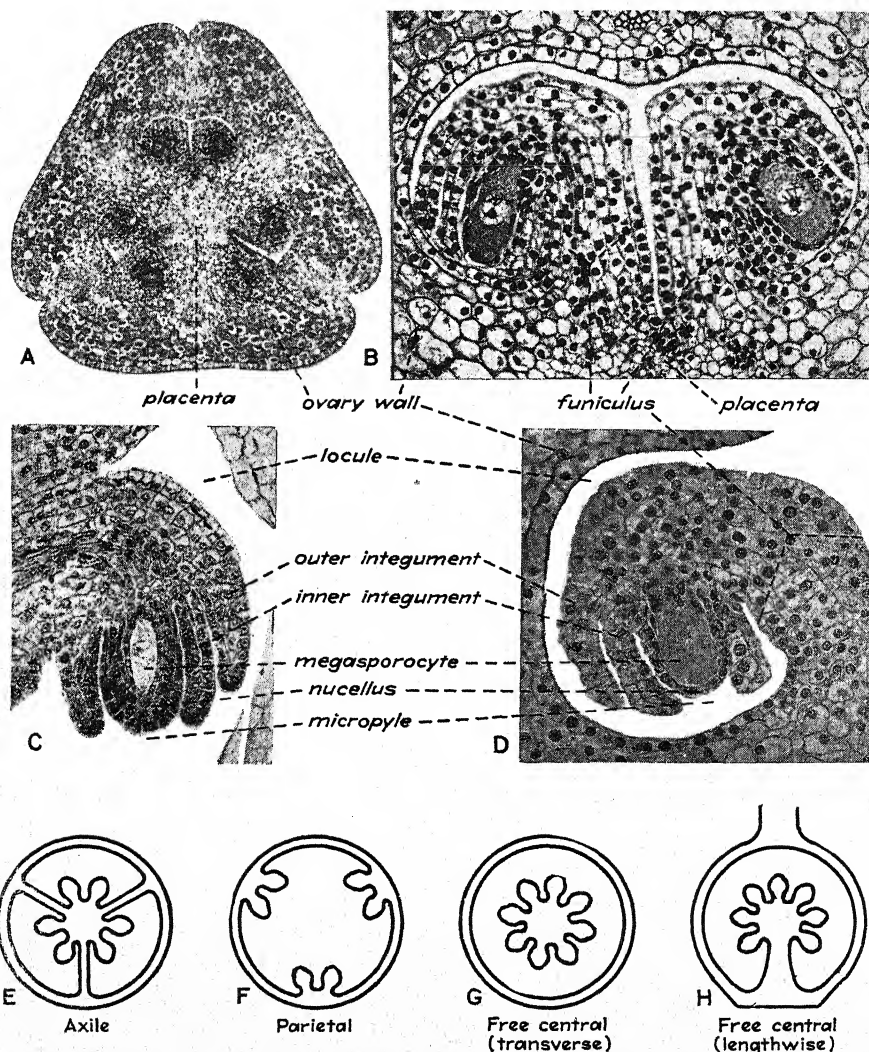


FIG. 107. Ovary and ovule structure; placentation. *A*, photomicrograph of a transverse section through a lily ovary showing axile placentation with two rows of ovules in each of the three locules; *B*, an enlarged view of one locule of the ovary of *A*, showing two ovules, each with a megaspore mother cell or megasporocyte; *C*, single ovule of *Fuchsia*, showing structure; *D*, single ovule of lily, showing structure; *E-H*, types of placentation, diagrammatically shown. (Photomicrographs *A-D* by D. A. Kribs.)

but the sepals and petals are radially arranged. The whole flower in this case is still said to have radial symmetry. In flowers with spirally arranged parts, there is usually a large and indefinite number of such parts.

Union of Flower Parts. In some flowers all the parts are attached directly to the receptacle and are entirely free from each other (Fig. 309, B, C). Thus there may be separate sepals (**polysepal**), separate petals (**polypetal**), separate stamens, and separate pistils. In others, the members of a whorl may be more or less united with each other, a condition referred to as **coalescence** of parts. Coalescence may involve sepals (**synsepal** or **gamosepal**), petals (**sympetal** or **gamopetal**), stamens, or pistils. In synsepalous flowers, the bases of the sepals are usually united in such a way as to form a cup, or **calyx tube**. Similarly, in sympetalous flowers a **corolla tube** may be formed. The flowers of the common Jimson weed (Fig. 311, G) have both a calyx tube and a corolla tube. The stamens may be united by their filaments into one (**monadelphous**), two (**diadelphous**) or several (**polyadelphous**) sets, as in members of the *Malvaceae*, *Leguminosae*, and *Tiliaceae*, respectively, or the anthers may be united (**syngenesious**) as in the Compositae. Union of pistils (**syncarpy**) occurs in all flowers with compound pistils.

In still other types of flowers, the members of one whorl of parts may be more or less united with members of another whorl, a condition called **adnation**. Thus the stamens may be attached to the petals as in flowers of the potato family (Fig. 311, C) and many other plants. In a few cases, as in orchids, the stamens are united with the carpels (Fig. 325, B). More frequently sepals, petals, and stamens are united at their bases, forming a cup, or **floral tube (hypanthium)**. In some cases, receptacle tissue may form a part of the floral tube. The floral tube is often called a calyx tube, but the latter term should be restricted to cases in which only the calyx is involved.

Hypogyny, Perigyny, and Epigyny. Depending primarily upon the apparent position of the other parts of a flower with respect to the ovary or ovaries, flowers may be **hypogynous**, **perigynous**, or **epigynous**. **Hypogynous** flowers are those in which stamens, petals, and sepals are attached to the receptacle below and entirely free from the ovaries of the pistils (Figs. 105, A; 108, C). This arrangement results in **superior** ovaries. The term is applied both to flowers with many separate pistils, like the buttercup (Fig. 309, C), and to flowers in which there is a single (simple or compound) pistil, as in peas (Fig. 315, F) and other legumes, which have a single, simple pistil, and in lilies (Fig. 105, A), which have a compound pistil.

In **perigynous** flowers there is a floral tube, or hypanthium. Within this tube or cup-like structure, but free from it, the pistil or pistils are

contained. The sepals, petals, and stamens appear to be borne on the margin or rim of the floral tube, but actually arise from the receptacle below the ovaries of the pistils. The ovaries therefore are superior as in hypogynous flowers. The cherry flower (Fig. 108, *D*) is a good example

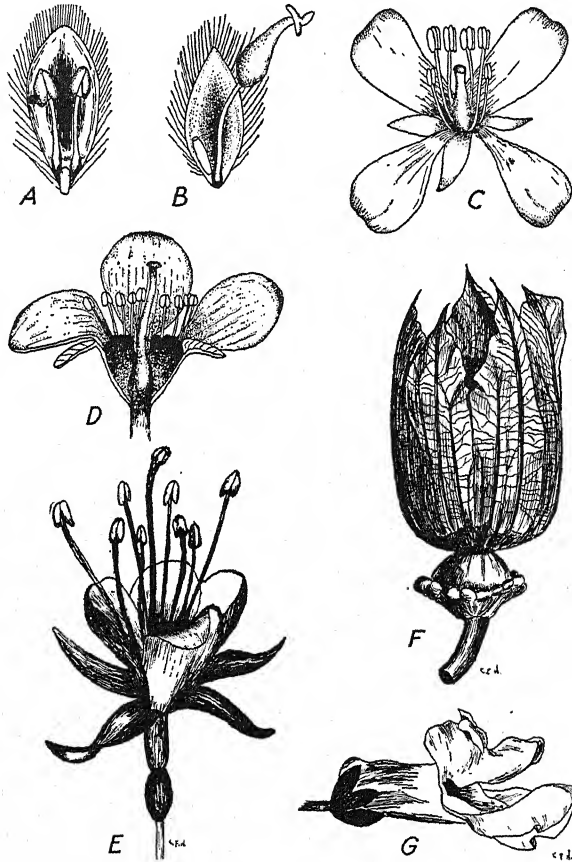


FIG. 108. Forms of flowers. *A*, a staminate flower of willow, consisting of two stamens borne in the axil of a scale-like, hairy bract; *B*, a pistillate flower of willow, consisting of a single-stalked pistil borne in the axil of a hairy bract; *C*, the hypogynous flower of *Cardamine*; *D*, the perigynous flower of cherry; *E*, the epigynous flower of *Fuchsia*, showing the inferior ovary borne below the other floral parts; *F*, the epigynous flower of the squash; *G*, the zygomorphic flower of snapdragon. (*A-D*, redrawn by Chris. Hildebrandt from drawings by Edna S. Fox; *E-G* by Chris. Hildebrandt.)

of this type. In the perigynous flowers of saxifrage the lower part of the ovary is united with the floral tube.

In **epigynous** flowers there is also a floral tube, but in this case the floral tube is united with (adnate to) the wall of the ovary, so that the other

floral parts appear to be attached to the top of the ovary (Figs. 108, *E*, *F*; 119, *A*). The ovary in this case is said to be **inferior**.

Many gradations occur between hypogyny and perigyny and between the latter and epigyny.

Development of Flowers on the Stem. A flower may be thought of as a specialized shoot consisting of stem and leaves. Sepals, petals, stamens, and pistils are thus merely leaves that specialize in carrying on reproduction. All are derived from primordial meristems. Flowers appear first as buds, either as separate flower buds or as parts of mixed buds. They originate either terminally on a stem or in a position corresponding to a leaf axil. The leaf primordium subtending the point of origin of a flower may or may not develop into a leaf. If it does and leaves are present on the flower cluster, they are usually of smaller size than the other leaves and are termed **bracts**. Occasionally these bracts are large, showy, and closely arranged so as to constitute the most conspicuous part of the flower cluster and are likely to be mistaken for petals, as in the Indian paintbrush (*Castilleja*), flowering dogwood, and *Poinsettia*. The chaff of grass is composed of bracts subtending flowers or flower clusters and the hooded portion (spathe) of the jack-in-the-pulpit is a single bract.

The various floral organs originate in a definite sequence at the apex of the floral stem. Sepals may appear first, followed by stamens, pistils, and petals, usually in that order. In the carrot family, the sequence seems to be stamens, petals, sepals, and pistil. In the apple, the order is sepals, petals, stamens, and pistils. At the outer edge of the receptacle, the sepal primordia are first seen as small protuberances of meristematic tissue at a number of points corresponding to the number of sepals that are to be developed (Fig. 109). These points of meristematic tissue are on a circle at the periphery of the receptacle. Elongation and differentiation in these several meristematic regions result in the development of the sepals. The members of the other floral sets originate in a similar manner and gradually assume their mature characteristics. The pistil or pistils occupy the central region, and therefore the apical growth of the central axis is usually stopped by their development. In this development of the flower, parts that are coalesced at maturity will be united from the beginning of their development. Similarly adnations are present from the start. The terms "united," "coalesced," "fused," and the like, as applied to floral parts, do not imply that these parts were at one time separate in the flowers in which they occur, although it is possible that they might have been separate in the remote ancestors of these flowers.

Inflorescences. Flowers are borne either singly, as in tulips, or in clusters, as in snapdragons. The flowering part of a plant, made up of

one or more flowers, and especially the mode of arrangement of the flowers, is called an **inflorescence**. The central axis of an elongated inflorescence is known as a **rachis**, and the primary stem which supports an inflorescence is termed a **peduncle**. If this stem or stalk arises from the ground level and is nearly or quite leafless, it may also be called a **scape**. The stems of the individual flowers of an inflorescence are called **pedicels**.

Two principal classes of inflorescences are commonly distinguished, viz., **indeterminate** inflorescences, in which the flowers occur in the axils of leaves, or bracts, arising from axillary buds, and **determinate** inflorescences, in which the flowers arise from terminal buds and thus terminate

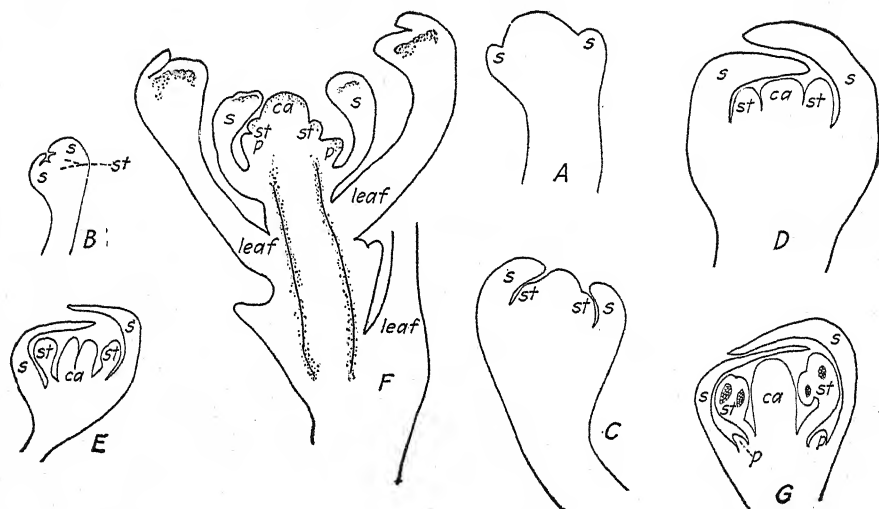


FIG. 109. Origin of flower parts in *Capsella*. A, sepals, *s*, first appear as small rounded swellings at the side of the stem apex; B, first appearance of stamens, *st*; C, sepal and stamen primordia enlarged; D, first appearance of carpels, *ca*; E, sepals, stamens, and carpels enlarging; F, diagram of longitudinal section through a greater portion of the stem apex, at this stage showing the first appearance of petal primordia, *p*; G, all parts enlarging.

a stem or branch. Some plants, like lilac and horse chestnut, have inflorescences which combine these two types and are sometimes called **mixed** inflorescences. In plants with indeterminate inflorescences, the terminal bud may keep on growing and prolong the stem indefinitely as in moneywort, but usually this is not the case. Among the inflorescences of the indeterminate class are the **spike**, the **catkin** or **ament**, the **spadix**, the **head**, the **raceme**, the **panicle**, the **umbel**, and the **corymb**. The solitary terminal flowers of some species and the **cyme** are examples of the determinate types of inflorescence. These various types are illustrated diagrammatically in Fig. 110. The different kinds of inflorescences are not always clearly distinguishable, nor can the distinction between determinate and indeterminate be made with certainty at all times.

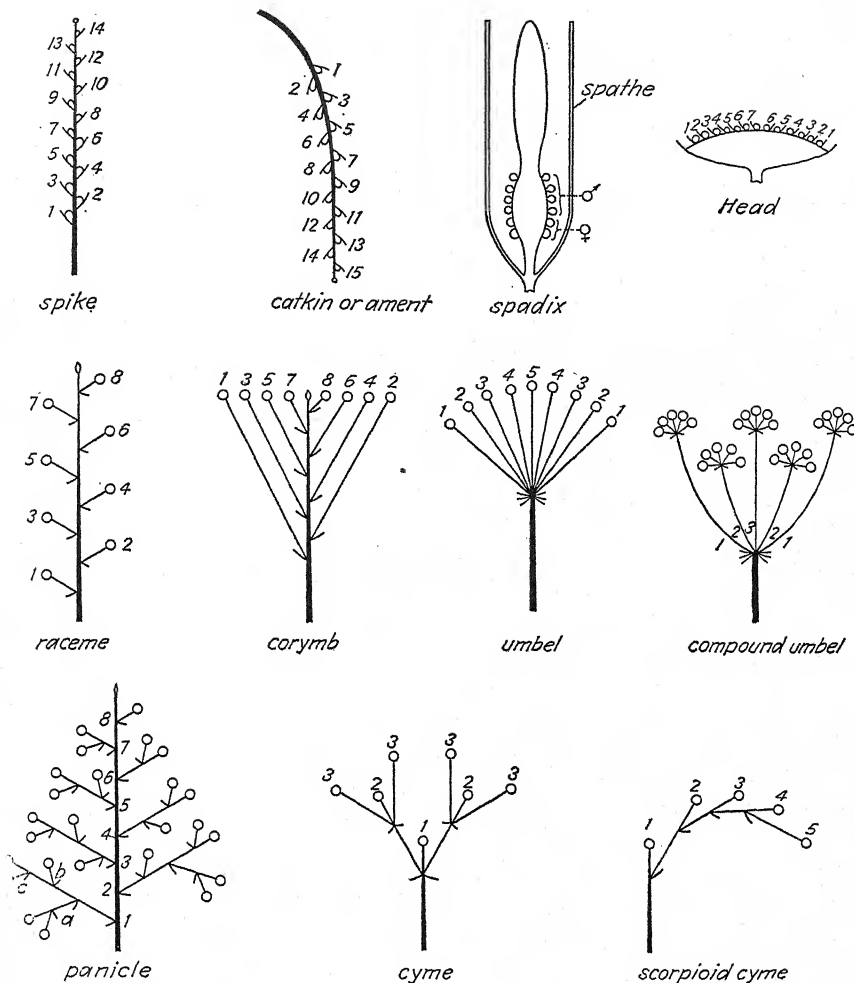


FIG. 110. Types of inflorescences, diagrammatically represented. Flowers are shown by small circles, and bracts by short, slightly curved lines. Figures indicate the usual sequence of opening of flowers, No. 1 opening first.

KINDS OF INFLORESCENCES

Indeterminate Inflorescences.

1. **Spike.** Flowers sessile on a more or less elongated axis, as in the common plantains.
2. **Catkin, or ament.** A scaly type of spike, often pendulous, usually consisting of either staminate or pistillate flowers, and characteristic of oaks, willows, poplars, birches and related species.
3. **Spadix.** A fleshy spike or head with small and usually imperfect flowers of both types commonly surrounded by an enveloping leaf or sheath, called the spathe, as in calla lily and jack-in-the-pulpit.

4. **Head.** A dense cluster of sessile or nearly sessile flowers on a very short axis, as in dandelion, sunflower, and other composites.
5. **Raceme.** Flowers borne on an elongated axis on pedicels more or less equal in length as in shepherd's purse and lily-of-the-valley.
6. **Panicle.** An inflorescence somewhat like a raceme in which the pedicels have branched so as to produce flowers on pedicels of their own, the branching being somewhat irregular, as in *Yucca* and many grasses.
7. **Umbel.** An inflorescence in which the pedicels all arise from a common point, as in onion. Compound umbels, as in carrot, are more common.
8. **Corymb.** Like a raceme but the pedicels of the flowers becoming shorter from the base toward the apex of the axis, resulting in a flat-topped or convex, open flower cluster, as in candytuft.

Determinate Inflorescences.

1. **Cyme.** Flowers arising from terminal buds, often forming a flat-topped or convex cluster in which the central flowers bloom first as in some members of the St. John's-wort and pink families.
2. **Scorpioid cyme.** A cyme in which one half of the cluster fails to develop, thereby forming a one-sided, coiled axis with the flowers on the convex side of the rachis, as in some members of the borage family.

REPRODUCTION BY FLOWERS

Since the parts of the flower have been described in the previous section, there remains to be considered how the flower carries on its functions in sexual reproduction. This involves a consideration of the development of pollen, pollination, the development of ovules, fertilization, the development of the embryo and endosperm, and finally the formation of fruit and seed.

Development of Pollen Grains. In the discussion on stamens, it was stated that the anther usually contains four elongated cavities, or pollen sacs, in which pollen grains are produced. An examination of these cavities while the anther is still young, usually while it is still in the flower bud, reveals the presence of many somewhat rounded cells called **microspore mother cells**, or **microsporocytes**. Each of the microspore mother cells, by two successive divisions, forms four cells, or **microspores** (Fig. 297, A-F). The microspore mother cells have the same number of chromosomes as do all ordinary cells of the plant. This number is commonly called the **diploid**, or $2N$, number. The process of division which takes place in the formation of microspores is called **meiosis** (see page 381) and results in the reduction of the chromosome number to the **haploid**, or $1N$, number, or half the diploid number. The microspores therefore are unicellular structures which have only half as many chromosomes as do the ordinary cells of the plant. The four microspores separate from each other, and each develops a characteristic shape or form which differs in different species of plants. The outer surface of the microspores may have spines, ridges, or furrows or may vary in other ways in different species.

About the time the anther splits open (dehisces), the single nucleus of each microspore divides by mitosis, forming a **generative nucleus** and a **tube nucleus** (Fig. 297, *H*), each of which has the haploid or $1N$ number of chromosomes. In this condition, the microspores have become **pollen grains** and are shed from the anther. Hundreds of pollen grains are usually produced in each anther.

Pollination. When the pollen grains are shed from the anther, they are disseminated by various agencies. Some of them may, by one means or another, finally reach the stigma of a pistil, either of the same or of another flower. *This transfer of pollen from anther to stigma is known as pollination.* Pollination ends when the pollen has reached the stigma. Plants are said to be **self-pollinated** when the pollen is transferred from an anther to a stigma of the same flower or to a stigma of another flower on the same plant; plants are **cross-pollinated** when the pollen from one plant reaches a stigma of a flower on another plant. Dioecious species are necessarily cross-pollinated. Monoecious species and plants with perfect flowers may be self-pollinated or cross-pollinated. Many, such as peas, tobacco, and many grasses, are commonly self-pollinated. Others, however, have devices that may induce cross-pollination where self-pollination might be possible. For example, the stigma may be receptive before the pollen in the same flower is mature; the anthers may mature and shed their pollen before the stigmas are receptive; the flower may be so constructed that there is little chance that pollen can be deposited on a stigma of the same flower; the flower may be sterile to its own pollen because of an inhibition either of germination or of the growth of the pollen tube down to the ovules of the same flower.

In securing the transfer of pollen, various agencies may be brought into play. Wind, water, insects, and even birds may act in this transfer. Many grasses and many trees are wind-pollinated. Flowers of these plants are often relatively inconspicuous, often without nectar glands, and produce great quantities of dry, powdery pollen. The stigmas are often feathery or much branched. The pollen grains of some wind-pollinated plants average around 0.025 mm. in diameter, and are sometimes, as in pines, provided with wings, which greatly facilitate their transport in air currents. Such pollen grains can be carried tremendous distances by the wind. How far they can be carried, however, is not so important a question as how long a period the pollen can remain viable when so carried. Under ordinary conditions, pollen remains viable for only a comparatively short time ranging from a few days to several weeks. Some water plants, such as pond lilies, elevate their flowers above the water thereby facilitating wind-pollination or insect pollination. Others (*Anacharis*) develop flowers just at the surface of the water, in such a position that pollen is readily

washed to them on the surface. Seed plants as a whole are probably more dependent upon insects than upon any other one agency for pollination. Many irregular flowers are so constructed as to be most efficiently pollinated by insects. This construction usually involves such form of the flower and position of the nectar glands as to result in the dusting of the insect with pollen on that part of its body that is most likely to come into contact with the stigma of the next flower visited. Many such flowers, can be pollinated only by certain kinds of insects. Thus the bumblebee is the only highly effective pollinating agent for red clover. Such flowers as snapdragons, in which the throat of the corolla is nearly closed, can be sprung open only by an insect of considerable size alighting on the lower lip of the flower. The *Yucca* flower can be pollinated only by the *Pronuba* moth, which at the same time lays its eggs in the ovary among the ovules, some of which later are used as food by the emerging larvae. There are many other interesting examples of this sort. Butterflies and hummingbirds are active agents in cross-pollination in certain special cases. The common honeybee is one of the most effective pollinators among insects.

Development of Cvules. As previously mentioned, an ovary may contain one or many ovules. Each ovule arises separately as a minute, dome-shaped projection from the placenta. Very early an undifferentiated, multicellular tissue known as the **nucellus** develops (Fig. 298, A). Beginning around the base of the nucellus, one or two layers of tissue called **integuments** gradually grow over its surface and eventually come to surround the nucellus, leaving only a small opening, the **micropyle** (Figs. 107; 298, C). The ovule is attached to the placenta by a stalk called the **funiculus** (Fig. 107), through which vascular strands extend to the ovule.

Before the integuments have enclosed the nucellus, there usually appears within the nucellus a single, large cell called the **megaspore mother cell**, or megasporocyte (Fig. 107, B), which by meiosis, consisting of two successive divisions during which the chromosome number is reduced by one half, gives rise to a row of four cells called **megaspores** (Figs. 298, C; 299, A-F), each of which has the haploid ($1N$) number of chromosomes. The basal one of the four, i.e., the one farthest from the micropyle, immediately begins to enlarge and becomes the functioning megaspore. The other three gradually disintegrate and disappear. As the ovule grows, the functioning megaspore continues to enlarge and its nucleus undergoes three successive mitotic divisions resulting in a structure consisting of eight haploid nuclei; four at the micropylar end of the ovule and four at the basal end (Fig. 300). One nucleus from each group of four now moves to the center. These are the **polar nuclei**. They may lie together, or they may fuse. The three nuclei left at the basal end are called **antipodals** and usually remain functionless. Of the three left at

the micropylar end of the ovule, one is the **female gamete**, or **egg**, and the other two are called **synergids** (helpers). The synergids later disintegrate. The whole structure, consisting of three antipodals, two polar nuclei, an egg, and two synergids, is now called the **mature female gametophyte**, a term which means a plant which produces female gametes. The female gametophyte is actually a greatly reduced female plant. Differences occur in different species of flowering plants in the manner in which the

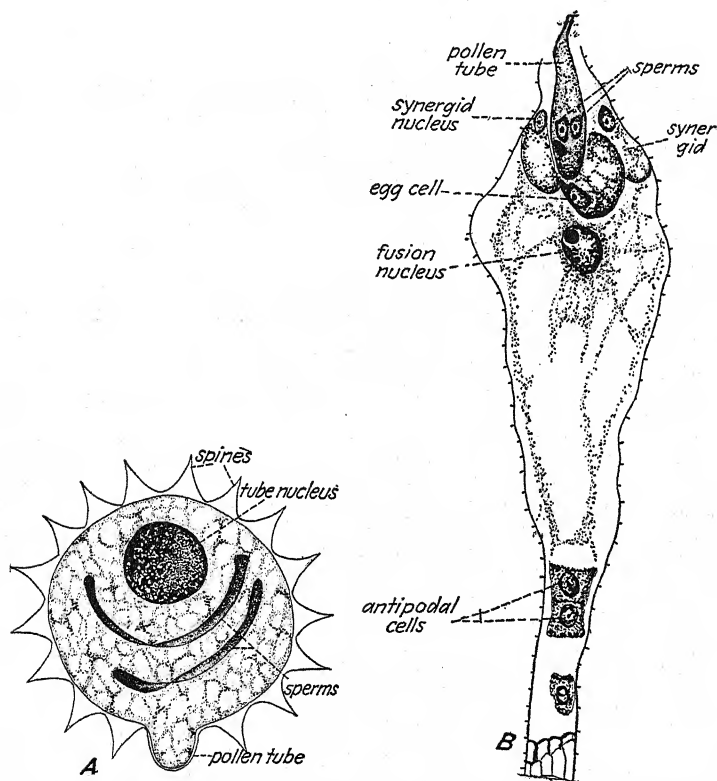


FIG. 111. Development of male and female gametophytes of *Silphium*; A, male gametophyte (germinating pollen grain); B, female gametophyte just before fertilization takes place.

female gametophyte develops, but the one just explained is common (see pages 619 to 630).

Events Culminating in Fertilization. When a pollen grain reaches a receptive stigma, it germinates by developing a slender tube called the **pollen tube**, which breaks through the wall of the pollen grain and penetrates the tissue of the stigma, ultimately growing down through the style (Fig. 111, A). The style may be hollow, but more often it consists of

solid tissue, in which case the pollen tube penetrates it by secreting enzymes which assist in dissolving away the stylar tissue as the pollen tube advances. Very soon after (and sometimes before) the pollen grain germinates, the generative nucleus divides to form two **male gametes**, or **sperms** (Fig. 111, A). These two sperms, together with the tube nucleus and most of the cytoplasm, keep moving down toward the tip of the pollen tube as it grows. Ultimately the pollen tube enters the locule of the ovary, grows through the micropyle of the ovule, penetrates the tissue of the nucellus, and finally reaches the female gametophyte (Fig. 111, B). The germinated pollen grain with its tube nucleus and two male-gametes, all of which are haploid ($1N$), is now the **mature male gametophyte**, or male gamete-producing plant. It is actually a greatly reduced male plant. On reaching the female gametophyte, the pollen tube usually enlarges and breaks at its tip, allowing the two male gametes, or sperms, to pass through. One of the sperms moves toward the egg and fuses with it. *This fusion of sperm and egg, and this alone, is fertilization.* The cell resulting from this fusion is called the fertilized egg, or **zygote**, and ultimately develops into an **embryo**, or young plant. Since the sperm and the egg are each haploid ($1N$), the zygote resulting from their fusion is diploid ($2N$), i.e., it has two sets of chromosomes, one contributed by the male parent and one by the female parent. The other male gamete moves to the center of the female gametophyte and fuses with the two polar nuclei or with the nucleus resulting from their fusion if this has occurred. The resulting nucleus is triploid ($3N$) and is called the **primary endosperm nucleus** because it gives rise to a nutritive tissue called **endosperm**. The tube nucleus usually disintegrates and disappears.

For each ovule that is to reach maturity in the ovary, a separate pollen grain must be provided. Thus it is not unusual to find many pollen tubes growing down through a single style. The time that elapses between pollination and fertilization varies from a few hours or days in some species to more than a year in others.

Development of the Embryo. Following fertilization, the fertilized egg, or zygote, initiates a series of divisions which lead to the development of the **embryo**. The female gametophyte now becomes the **embryo sac**, or structure in which the embryo is originally contained. Generally, two or three early divisions follow each other in rapid succession resulting in the production of a tier of three to five or more undifferentiated cells called the **proembryo**. The proembryo gradually becomes differentiated into recognizable parts or regions. The exact method of origin of these parts and the final form of the embryo vary in the different groups of seed plants. Certain features, however, are fairly common to the group. Quite early, the basal cell of the embryo becomes attached to the wall of the embryo

sac and enlarges (Fig. 112). The terminal cell of the proembryo becomes the embryo proper, and the cells below constitute the **suspensor**. The suspensor, characteristic of the embryos of almost all flowering plants, may consist of but a few cells forming a short, slender filament; it may become thick and massive; or it may consist of several to many (12 to 20) cells.

In dicotyledons, such as *Capsella*, which is commonly used to illustrate embryo development, the embryo proper develops from the terminal cell of the proembryo as stated above. Division in the terminal cell is first longitudinal, resulting in the formation of two cells. Other divisions follow quickly and result in the formation of eight cells arranged in two tiers of four cells each (Fig. 112, C). The outer or terminal four cells form the **plumule**, or first vegetative shoot of the embryo, and the two **cotyledons**, or seed leaves. The second tier forms the **hypocotyl**, or stem of the embryo below the cotyledons. The tip of the root, or **radicle**, formed on the lower end of the hypocotyl and adjacent to the suspensor, is completed from the upper adjacent cell of the suspensor. The completed embryo (Fig. 112, G) thus consists of a stem, or hypocotyl, bearing at its tip a growing point, or plumule, and, as is common with dicotyledons, two cotyledons. (In monocotyledons only one cotyledon is formed.) In addition to these structures, there is an embryo root, or radicle, on the basal end of the hypocotyl. The suspensor is attached to the root tip and in *Capsella* can be seen clearly in the mature embryo.

The degree to which the embryo develops before the seed ripens varies greatly in different plants. In some cases, it develops only a little beyond the proembryo stage. In others, all the organs mentioned are formed, and the embryo may occupy the entire embryo sac.

Formation of Endosperm. Immediately following fertilization and often before the embryo starts to develop, the endosperm nucleus undergoes a series of divisions that result in the development of many free nuclei. Later, cell walls develop between the nuclei. In this way, a storage tissue called the **endosperm** is developed, in which reserve food, available for the growing embryo, is stored. In most plants the endosperm in its growth replaces all the nucellus tissue, but in a few cases, like that of certain water lilies, the nucellus persists and forms a considerable part of the mature ovule. The endosperm itself may be entirely consumed by the developing embryo or may remain as a food-storage tissue. In peas, beans, and other legumes, the endosperm disappears entirely before the ovule ripens. In the morning-glory, the castor bean, and all grasses, the endosperm persists in the fully ripened ovule.

Formation of Fruit and Seed. During the growth of the embryo and endosperm, there is also a rapid growth of the other tissues of the ovule

and an increased translocation of foods to the embryo sac. The ovule usually increases markedly in size, and many physical and chemical changes take place in its tissues. The integuments expand and then frequently

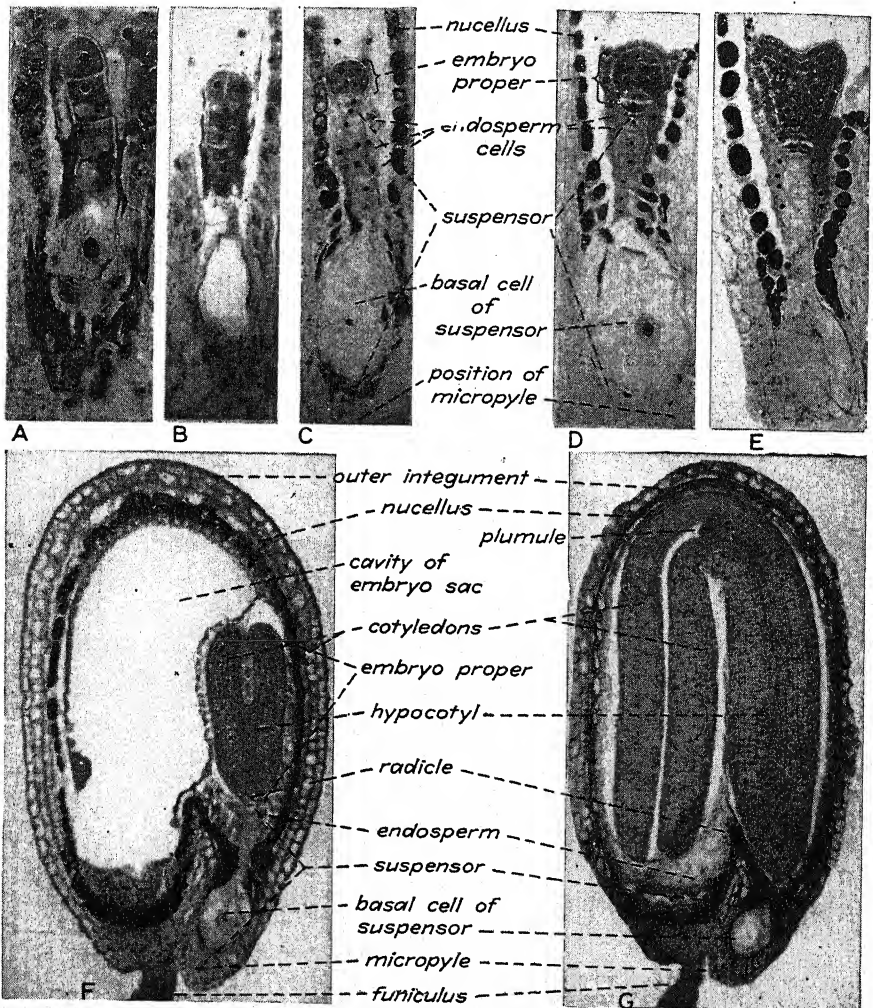


FIG. 112. Photomicrographs showing development of the embryo in *Capsella*; A, proembryo; B-G, successive stages under decreasing magnification; F and G, lengthwise sections of entire ovules showing position of embryo within the ovule. (Photomicrographs A-E, by D. A. Kribs.)

harden and dry out. Soluble foods carried into the ovule are converted into insoluble storage forms. Thus sugars may be converted into starch, amino acids into proteins, and fatty acids and glycerol into fats and oils.

The relative amount of water in the tissues decreases, and the ovule gradually changes from a relatively soft, succulent structure to a hard, relatively dry body. As this development progresses, the physiological activity within the ovule gradually decreases and the embryo becomes dormant. The ovule thus ripens into a **seed** in which the integuments become protective seed coats, and the interior is occupied by a resting embryo together with stored food. This food may still remain in the endosperm tissue or it may be stored entirely in the embryo itself.

Fertilization stimulates a rapid growth of the whole ovary as well as the ovules. Such flower parts as the stamens, petals, and sepals, together with the stigma and style of the pistil, usually wither and fall off after pollination and fertilization take place, although in some plants the bases of the stamens, petals, and sepals or the receptacle may be stimulated to renewed growth and development. In some cases, the style of the pistil may likewise be retained and enlarged. The ovary usually increases greatly in size, and its tissues may become highly differentiated in the production of parts concerned with the protection and the dissemination of the seeds. The mature ovary containing the seeds, together with any accessory structures developed from the receptacle or other parts, is now called the **fruit**. The different kinds of fruits are described in the following chapter.

When fertilization fails to occur, the entire flower usually dies, or as is commonly stated the flower fails to "set fruit." Thus there are seldom as many fruits on a plant as there were flowers. There are some plants, however, that produce fruits regularly even though fertilization has not taken place. This condition is known as **parthenocarpy**, and the fruits so produced are said to be **parthenocarpic**. Among the plants which normally develop parthenocarpic fruits may be mentioned the common banana, the navel orange, the seedless raisin grape, and the pineapple. In recent years, parthenocarpic fruits have been produced artificially by spraying, or applying in other ways, certain chemicals (growth substances) to the pistils of the flowers or to the ovaries directly. In this way, seedless tomatoes, cucumbers, peppers, melons, and other fruits have been produced (Fig. 95, I, C; II).

The development of seeds and fruits is an exhaustive process which usually checks the growth of the vegetative organs of the plant. Annual plants usually die soon after the seeds and fruits are matured. In such plants the seeds alone remain living and serve to perpetuate the species.

CHAPTER 11

FRUITS, SEEDS, AND SEEDLINGS

FRUITS

Definition. Botanically, a fruit is a matured ovary with or without seeds. In many fruits, however, other structures derived from other flower parts or from the axis (receptacle) tissue may become a part of the fruit. Thus in fruits derived from inferior ovaries, the enlarged hypanthium, or floral tube, is usually still present in the fruit. In some cases, these accessory structures may become a prominent part of the fruit, as in apples and pears. Furthermore, a fruit may consist of several matured ovaries remaining together as a unit and may even include the matured ovaries of an entire inflorescence. *A fruit may therefore be defined as a structure made up of one or more matured ovaries together with any accessory structures closely associated with them.*

From the definition of a fruit it is clear that the popular use of the term does not always coincide with the botanical. Thus tomatoes, cucumbers, snap beans, pea pods, peppers, squashes, and many kinds of nuts that appear in our markets are botanically fruits. Furthermore, many single-seeded fruits, like those of lettuce, buckwheat, sunflower, and grains like corn and wheat are commonly sold in the markets as seeds (Fig. 113). The fact that they are all matured ovaries clearly proves that all these examples are fruits.

Structure of the Pericarp. The matured wall of the ovary in the fruit is called the **pericarp**. The structure of the pericarp varies greatly in different kinds of fruits. In some, three distinct layers may be differentiated, *viz.*, an outer layer called the **exocarp**, a middle layer called the **mesocarp**, and an inner layer called the **endocarp**. The **exocarp**, though sometimes more complex, often appears as a single layer of epidermal cells, sometimes heavily cutinized and sometimes hairy. The **mesocarp**, or middle layer, may be very thin or it may be a well-developed tissue several centimeters thick. It usually contains vascular bundles, and in some fruits it is fleshy. The **endocarp** also varies greatly in structure in different fruits; sometimes it consists of a single layer of cells and sometimes of many layers. In some fruits, the endocarp becomes very tough or hard. In others, it is fleshy. These three layers are most clearly differentiated in such fruits as peaches, plums, and cherries in which the fleshy part of the fruit is the mesocarp.

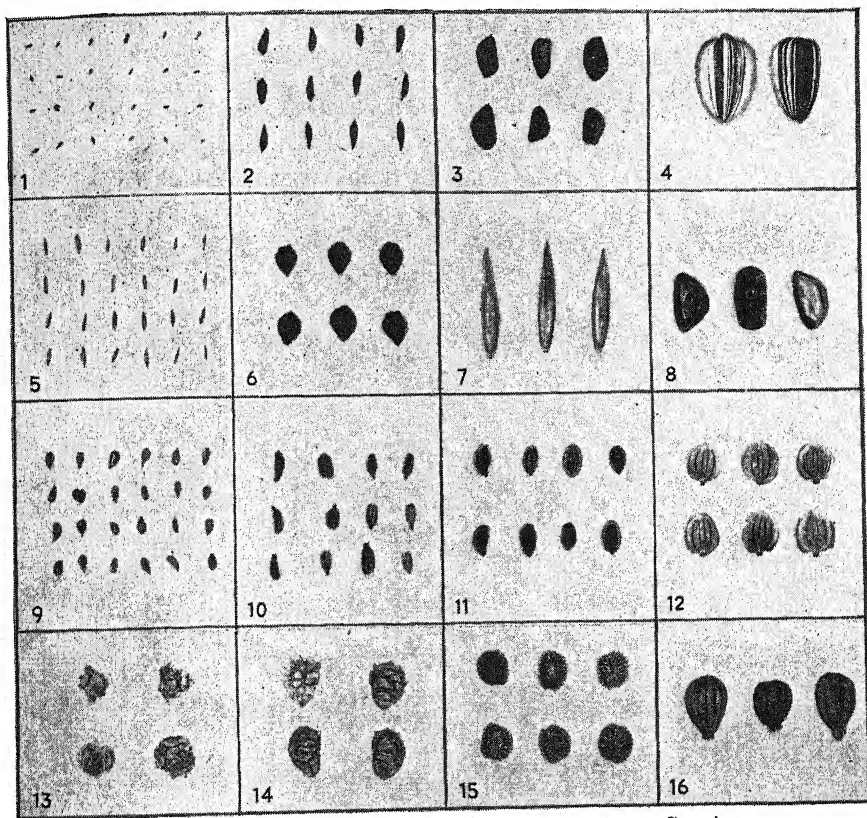


FIG. 113. Seed-like fruits. (Photograph by Homer Grove.)

Top Row, Achenes

- 1, Wormwood (*Artemisia Absinthium*); 2, lettuce (*Lactuca sativa*); 3, rose (*Rosa rugosa*); 4, sunflower (*Helianthus annuus*).

Second Row, Grains

- 5, Kentucky blue grass (*Poa pratensis*); 6, sorghum (*Sorghum vulgare*); 7, oats (*Avena sativa*); 8, teosinte (*Euchlaena mexicana*).

Third Row, Mericarps

- 9, parsley (*Carum Petroselinum*); 10, carrot (*Daucus Carota*); 11, dill (*Anethum graveolens*); 12, parsnip (*Pastinaca sativa*).

Fourth Row, Miscellaneous

- 13, beet (*Beta vulgaris*), multiple fruits, commonly called "seed balls"; 14, Sainfoin (*Onobrychis viciaefolia*), a one-seeded legume; 15, French honeysuckle (*Hedysarum coronarium*), segments of loments; 16, European hornbeam (*Carpinus Betulus*), a winged, nut-like fruit with the wings removed.

In some fruits, and particularly those arising from inferior ovaries, the floral tube may persist in the fruit, forming the outermost layers of the fruit. In such cases, the pericarp may be difficult to differentiate.

KINDS OF FRUITS

Fruits are of many kinds. The structure of a fruit can only be understood by a knowledge of the structure of the flower from which the fruit arises. The presence of accessory structures in a fruit may obscure the true nature of the fruit in its mature condition and may render the fruit difficult to classify unless its development is followed step by step from the flower. Even then, different interpretation of structures by different investigators may lead to difficulties in classification.

In general, all fruits may be classified into three groups: (1) **simple fruits**, which are developed from a single (simple or compound) pistil and thus consist of a *single matured ovary* together with any accessory structures closely associated with the ovary; (2) **aggregate fruits**, which consist of a *number of matured ovaries* aggregated as a unit on a common receptacle, together with any accessory structures, all developed from a *single flower* with many separate pistils, as in raspberries and blackberries; (3) **multiple fruits**, which consist of all the matured ovaries of *several flowers* grouped into a single mass, together with any accessory structures, the whole being developed from an entire inflorescence as in pineapples, mulberries, and figs.

The term **accessory fruit** is sometimes applied to fruits in which a major part of the matured fruit has not developed from the ovary. This type of fruit does not represent a group distinct from the three just mentioned but is represented in all three groups. Thus the simple fruit of the apple, the aggregate fruit of the strawberry, and the multiple fruit of mulberry are all accessory fruits. The major portion of the fleshy part of an apple fruit consists of the enlarged bases of the sepals, petals, and stamens, the fleshy part of the strawberry is the receptacle, and in the mulberry the fleshy sepals form a considerable part of the fruit.

Of the three groups mentioned, simple fruits are by far the largest group and the most diversified. They may be subdivided into **dry fruits**, those in which the pericarp and any accessory structures become more or less dry when mature, and **fleshy fruits**, those in which a part or all of the pericarp and any accessory structures become fleshy at maturity. The dry fruits are further subdivided into **dehiscent fruits**, those which split open at maturity, and **indehiscent fruits**, those which do not split open at maturity. The line (or lines) along which a dehiscent fruit opens at maturity is called a **suture**, and the resulting segments of the pericarp are known as **valves**.

Simple, Dry, Dehiscent Fruits. *Legume.* The legume fruit is characteristic of the members of the legume or pea family. In legume flowers, such as those of the pea (Fig. 114, *B*), the gynoeceium consists of a single, simple pistil with a superior ovary containing a single cavity, or locule. By the maturation of this pistil, the fruit, or pod, is formed (Fig. 114, *A*, *C*). The remains of stigma and style can often be seen at the free end of the pod. The seeds are developed along the ventral suture, which is the one along which the margins of the carpel are united. The dorsal suture corresponds to the midrib of the carpel. At maturity the fruit splits along both dorsal and ventral sutures into two valves. Some leguminous plants have fruits that show considerable variation from this type. In tick trefoil (*Desmodium*) the fruits are constricted between the seeds and finally break up crosswise into distinct parts. A legume of this type is called a **loment**. Some legume fruits are single-seeded. Others have many seeds. The legume is distinguished from other simple, dry, dehiscent fruits by the fact that it develops from a simple pistil and splits open at maturity along both dorsal and ventral sutures.

Follicle. The follicle resembles the legume in that it develops from a single, simple pistil but differs from the legume in that it splits open at maturity along only one suture. Examples of follicles are the fruits of larkspur (Fig. 114, *F*, *G*) columbine (Fig. 114, *E*, *I*), and milkweed (Fig. 114, *H*).

Capsule. The capsule differs from the legume and the follicle in that it is developed from a *compound pistil*. Any simple, dry dehiscent fruit that develops from a compound pistil may be called a capsule (Fig. 115). Capsules therefore always consist of two or more ovarian segments, which are the ovaries of the individual carpels. At maturity, a capsule may open by means of pores, as in poppy (Fig. 115, *E*) (**poricidal dehiscence**), or by a regular transverse circular line of division, as in purslane (*Portulaca*) (Fig. 115, *A*, *B*) (**circumscissile dehiscence**). The latter type of capsule is called a **pyxis**. More commonly, capsules dehisce by lengthwise division into valves. If the lengthwise splitting occurs down the back, or dorsal, suture of each ovarian segment directly into the loculi, as in Iris and lily, the dehiscence is said to be **loculicidal** (Fig. 115, *G*, *g*); if the splitting occurs along the ventral suture of each ovarian segment, through the partitions and between the loculi, thus dividing the capsule into its component ovarian segments, as in St.-John's-wort and some species of *Yucca*, the dehiscence is **septicidal** (Fig. 115, *H*, *h*). When the valves of either of the last two types break away from the partitions, these remaining attached to the axis of the fruit, as in morning-glory, the dehiscence is **septifragal** (Fig. 115, *I*, *i*).

The fruits of members of the mustard family (*Cruciferae*) are capsules

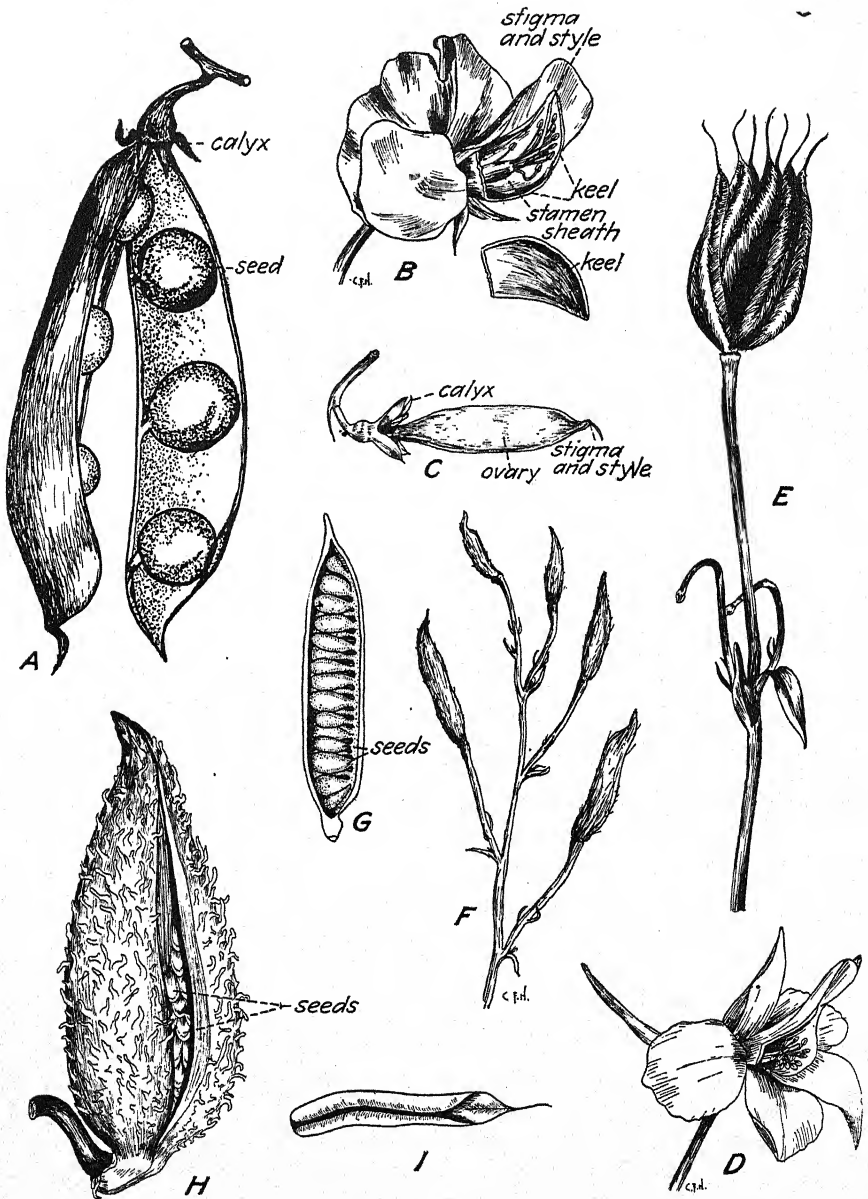


FIG. 114. Legumes and follicles. *A*, mature legume fruit (pod of pea); *B*, flower of pea with portion of keel cut away to expose the essential organs; *C*, young pod of pea; *D*–*I*, follicles; *D*, flower of larkspur with one side of a petal removed to show several stamens and pistils; *E*, mature follicles of columbine, all from one flower; *F*, follicles of larkspur; *G*, follicle of larkspur in longitudinal section; *H*, follicle of milkweed beginning to open; *I*, old follicle of columbine that has opened and discharged the seed. (*A*, *B*, *E*, *H*, drawn by Elsie M. McDougale; *C*, *D*, *F*, *G*, by Chris. Hildebrandt.)

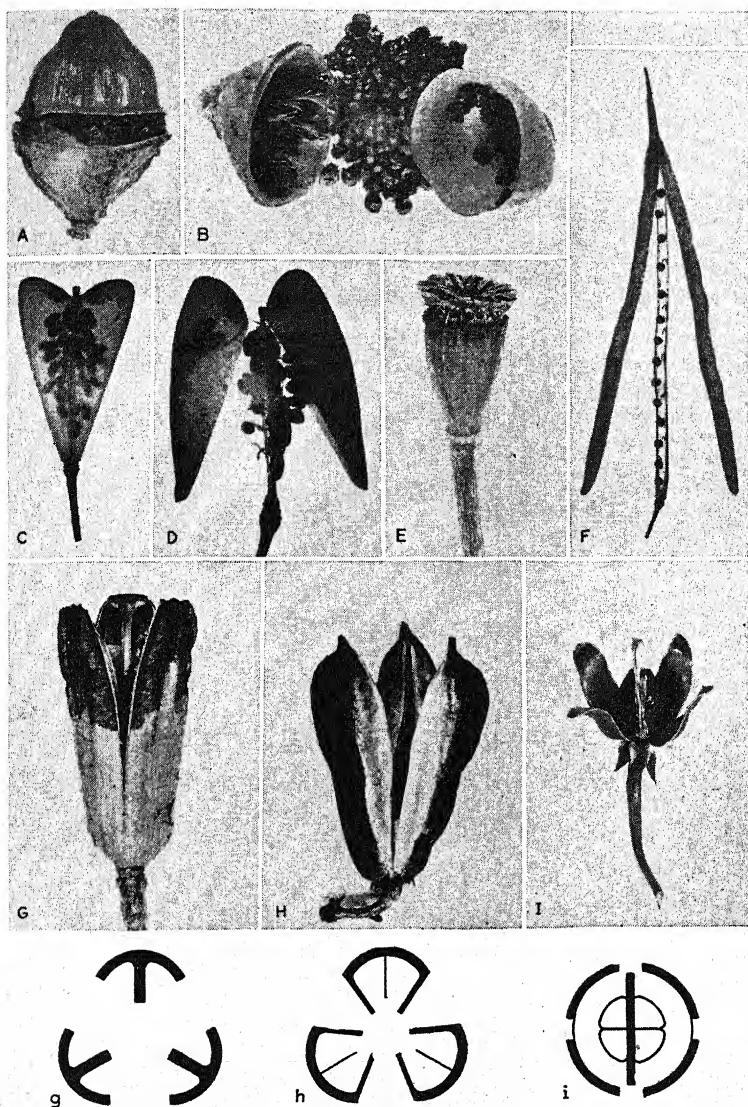


FIG. 115. Capsules. A, pyxis of *Portulaca* showing circumscissile dehiscence; B, the same opened, showing discharged seeds (both A and B greatly enlarged); C and D, silicle of shepherd's-purse; C, before opening; D, showing dehiscence from below upward, exposing the seeds; E, capsule of poppy showing poricidal dehiscence; F, silique of rutabaga; G, capsule of lily showing loculicidal dehiscence; H, capsule of a species of *Yucca* showing septicidal dehiscence; I, capsule of morning-glory opened to show septifragal dehiscence; g, h, and i, diagrams of transverse sections of G, H, and I, respectively, with seeds removed in g and h. The four central structures in i are seeds. (Photographs E-I by Homer Grove.)

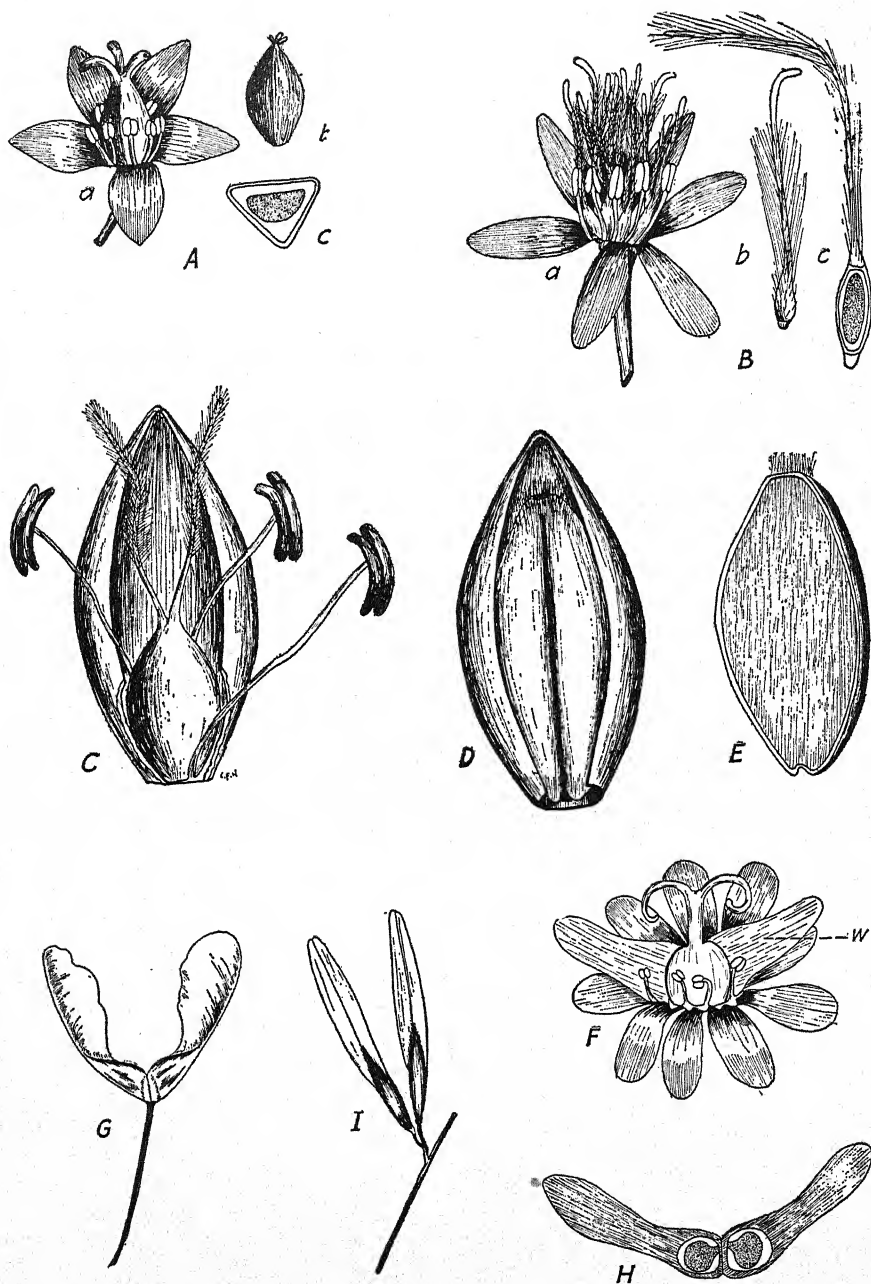


FIG. 116. Achenes, grains, and samaras. A, flower and achene type of fruit of buckwheat; a, flower of buckwheat, showing sepals, stamens, and the pistil with three styles and stigmas; b, the mature three-angled fruit with remnants of styles at apex; c, cross section of the fruit

consisting of two ovarian segments which separate at maturity into two valves opening from below upward, exposing a thin partition with the two placentae to which the seeds are attached. This type of capsule is called a **silique** if it is much longer than broad, as in cabbage, rutabaga, and *Cardamine* (Fig. 115, *F*), and a **silicle** if it is short and broad, as in shepherd's-purse (Fig. 115, *C, D*).

Simple, Dry, Indehiscent Fruits. *Achene.* **Achenes** (Figs. 113; 116, *A, B*) are small, dry, indehiscent, one-seeded fruits in which the seed is attached to the pericarp at only one point. They are derived from simple pistils containing only one ovule. This type of fruit is characteristic of the buckwheat and sunflower families and occurs also in the buttercup and rose families. Some achenes, like those of buckwheat (Fig. 116, *A, b, c*), are derived wholly from ovary tissue, while in others, such as members of the sunflower family, the floral tube is fused to the pericarp. Since the seed is attached at only one point, the pericarp is readily separable from the seed coat. Achenes are popularly mistaken for seeds.

Grain, or Caryopsis. **Grains** (Fig. 116, *C-E*), like achenes, are simple one-seeded, dry fruits derived from single, simple pistils, but differ from achenes in that in grains the seed coat is permanently fused to the pericarp over its entire surface, and thus cannot be easily separated from the seed. Grains are characteristic of all grasses, such as corn, wheat, oats, barley, rice, and rye.

Samara, or Key Fruit. The **samara** (Fig. 116, *F-I*) is essentially a winged achene, although the term is sometimes used for any indehiscent dry fruit furnished with a wing. It is the characteristic fruit of maples and ashes and occurs also in elms, birches, and in the tree of heaven (*Ailanthus*). The wing is usually an outgrowth of the ovary wall. In some cases, as in elms and birches, the wing extends all around the pericarp. In ashes and maples, it develops on one side only. In maples, two carpels develop side by side, each forming a samara. For this reason, the maple fruit is sometimes called a double-key fruit. The two parts may separate at maturity. Samaras usually have only one seed but occasionally have two.

with the single seed; *B*, flower and achene fruit of *Clematis*; *a*, flower, showing six petal-like sepals, a circle of several stamens, and numerous simple separate pistils clothed with long hairs below the protruding stigmas; *b*, a single pistil; *c*, a pistil with the ovary cut vertically to show the single locule and the single seed; the persistent styles become plumose in the fruit; *C*, flower of wheat, showing the three stamens and the single pistil with two plumose styles partially enclosed by the chaffy bract; *D*, the maturing wheat grain enclosed in the bract; stamens and stigmas have disappeared; *E*, longitudinal section of the grain; the outermost layer is the pericarp; *F*, flower of maple showing sepals, stamens, and the pistil with two styles and stigmas, the wall of the ovary having grown out on either side to form the characteristic wing, *w*, of the samara fruit; *G*, mature samaras of maple; *H*, mature ovaries of maple samaras cut lengthwise to show the single seed in each; *I*, mature samaras of ash. (*A-F* and *H* drawn by Chris. Hildebrandt; *G, I*, by Elsie M. McDougale.)

Schizocarp. The **schizocarp** (Fig. 117) is the characteristic fruit of the carrot family. It consists of two ovarian segments, each of which has a single locule usually containing a single seed. The ovarian segments of the fruit separate, each half being called a **mericarp**, which is indehiscent and resembles an achene. The fruits of mallows are of similar structure but involve a number of ovarian segments each containing one to several seeds.

Nut. **Nuts** (Fig. 118) are dry, indehiscent fruits in which the pericarp is hard or crustaceous throughout. At maturity, they commonly have but one locule and one seed but are usually developed from a compound pistil only one carpel of which develops. Examples are acorns, beech-nuts, hazelnuts, and chestnuts. All these examples are developed from inferior ovaries and hence the wall of the fruit consists of the floral tube as well as the pericarp, both being hard. In addition, all have at the base

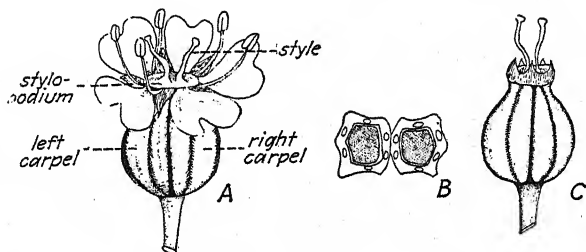


FIG. 117. The schizocarp fruit of the carrot family. A, flower of *Cicuta*; B, cross section of fruit, showing the two ovarian segments insecurely attached to each other and the single seed in each; C, ripening schizocarp of *Cicuta*; the free part of the calyx shows as a crown of five small lobes at top of the inferior ovary. (Copied by Chris. Hildebrandt from drawings by Edna S. Fox.)

an **involucre**, which is an accessory structure not developed from the ovary. The cup of the acorn is the involucre. It consists of numerous coalesced bracts (Fig. 118, *F-I*). In the beech, two separate one-seeded fruits, each coming from a separate flower, are usually enclosed within a single involucre (Fig. 118, *A-E*). The structure of the chestnut is similar, but each bur (involucre) usually encloses three nuts. In the hazelnut (Fig. 118, *J, K*), the involucre is made up of leafy bracts. Popularly, the term "nut" has been applied to many structures that botanically are not this type of fruit. Thus peanut pods are legumes, Brazil nuts are seeds, and almonds are parts of drupes.

Simple, Fleshy Fruits. **Pome.** Pome fruits (Fig. 119) are characteristic of that portion of the rose family to which the apple, pear, and quince belong. The fruit is developed from a compound pistil consisting of two or more carpels and an inferior ovary. The fleshy outer portion of the fruit develops from the bases of the calyx, corolla, and stamens (hypan-

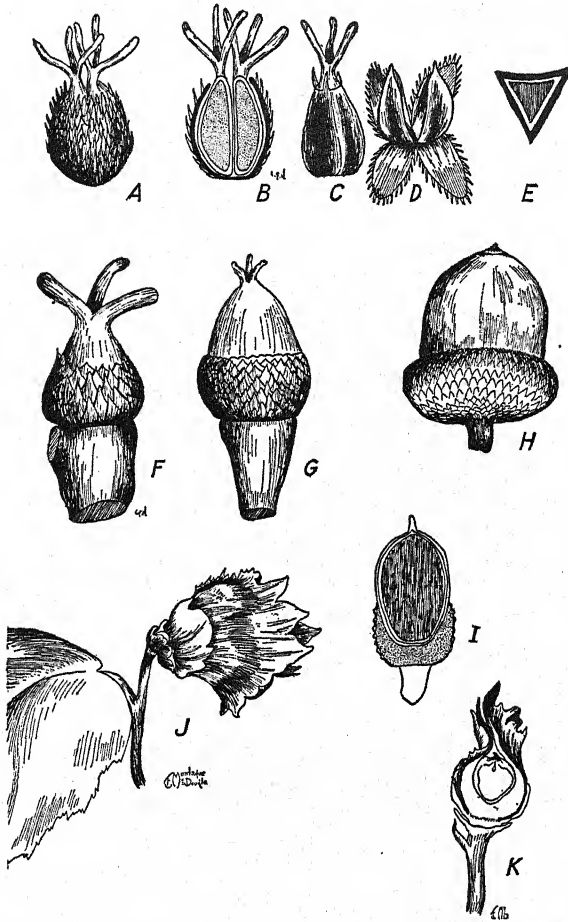


FIG. 118. Fruits of the nut type. *A*, two pistillate flowers of beech surrounded by bristly involucre bracts, with only stigmas and styles protruding; *B*, beech flowers cut vertically, showing the ovary and the three styles of each of the two flowers; *C*, single flower of beech taken out of the involucre bracts; the presence of a calyx is plainly indicated by the three small calyx lobes below the bases of the three styles; *D*, bur of beechnut at time of ripening of the two nuts; *E*, cross section of the triangular nut, showing the single seed, *F*, oak pistillate flower composed of a single pistil with three styles, surrounded by the closely set bracts that form the cup; *G*, more mature pistil in cup; *H*, mature acorn fruit in cup; *I*, vertical section through fruit and cup of acorn, showing the single large seed filling the nut; *J*, the hazelnut fruit entirely enclosed in the prominent involucre bracts; *K*, vertical section through hazelnut with its single seed. (*A-G* by Chris. Hildebrandt; *H-K* by Elsie M. McDougale.)

thium) which surround the ovary. The outer part of the pericarp also becomes fleshy, while the endocarp becomes more or less cartilaginous, forming the core of the fruit, containing several to many seeds. Since a major part of the fruit is not developed from the ovary, the pome is an accessory fruit.

Drupe. The **drupe** (Fig. 120, A-C), commonly called a "stone fruit," is a fleshy fruit in which the pericarp consists of a thin exocarp, usually skin-like, a fleshy mesocarp, and a hard, stony, endocarp, as in cherries, plums, and peaches. In the examples mentioned, the fruits develop from single, simple pistils of perigynous flowers (Fig. 108, D). Since these all have superior ovaries, no accessory structures are present in the fruit. Usually only one seed develops within the ovary. Some drupaceous fruits, however, develop from inferior ovaries and several carpels may

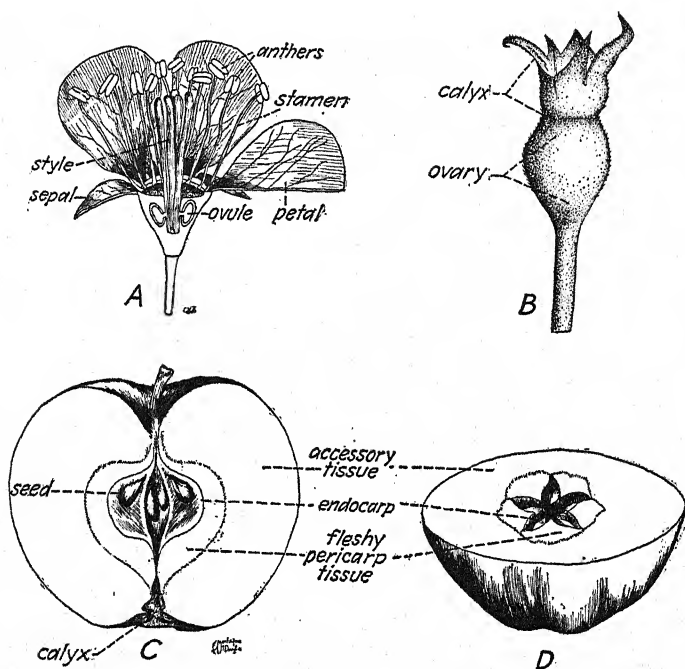


FIG. 119. The pome fruit (apple). A, apple flower cut vertically; B, young apple fruit; C, apple fruit cut vertically; D, apple fruit cut transversely. (A, B, copied by Chris. Hildebrandt from drawings by Edna S. Fox; C, D, by Elsie M. McDougale.)

originally be involved, as in *Viburnum*. Usually only one carpel matures. The almond, the olive, and the apricot are also drupes.

Berry. The **berry** is a simple fleshy fruit in which all parts of the pericarp are fleshy or pulpy except the exocarp which is often skin-like. Berries originate from flowers with simple or compound pistils, the ovaries of which may have one or many ovules. More often the fruits are many-seeded. Grapes, tomatoes (Fig. 120, D, E), gooseberries, and cranberries are true berries. In the grape and in the tomato, the fruit is developed from a superior ovary, while in the cranberry and in the gooseberry it

develops from an inferior ovary. In the latter case, the floral tube invests the matured ovary externally.

The fruit of squashes, pumpkins, cantaloupes, watermelons, and cucumbers is a berry invested with a rind that is not readily separable from the pericarp. The rind is made up mostly of floral tube tissue. This type of fruit is called a **pepo**. Similarly, the fruit of oranges, lemons, and grapefruit is surrounded by a leathery rind (in this case part of the pericarp

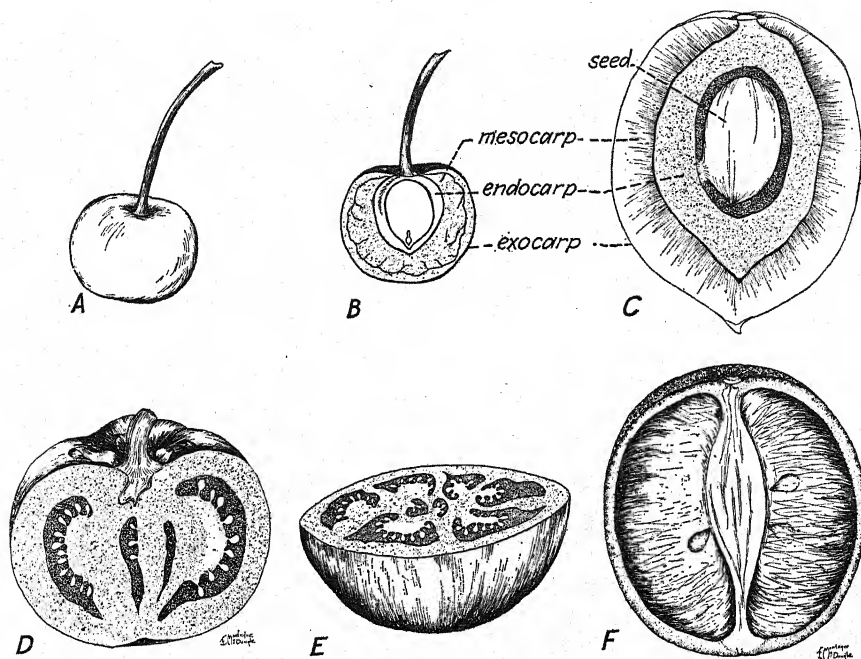


FIG. 120. Drupes and berries. A, external view of drupe fruit of cherry; B, cherry cut vertically; C, drupe fruit of peach cut vertically; D, E, the berry type of fruit; D, vertical section of a tomato; ovary fleshy throughout; E, transverse section of the tomato; F, the orange, a hesperidium, or berry with a leathery, separable rind, cut vertically. (Drawings by Elsie M. McDougale.)

since the ovary is superior) which is separable. This fruit is called a **hesperidium** (Fig. 120, F).

From the description just given, it is clear that the popular use of the term "berry" does not always coincide with the botanical. Mulberries, strawberries, blackberries, and raspberries are not berries in the botanical sense.

Aggregate Fruits. Aggregate fruits are derived from single flowers with many separate pistils (Fig. 121, A, B) and thus consist of a number of similar small fruits all on a common receptacle and maturing together

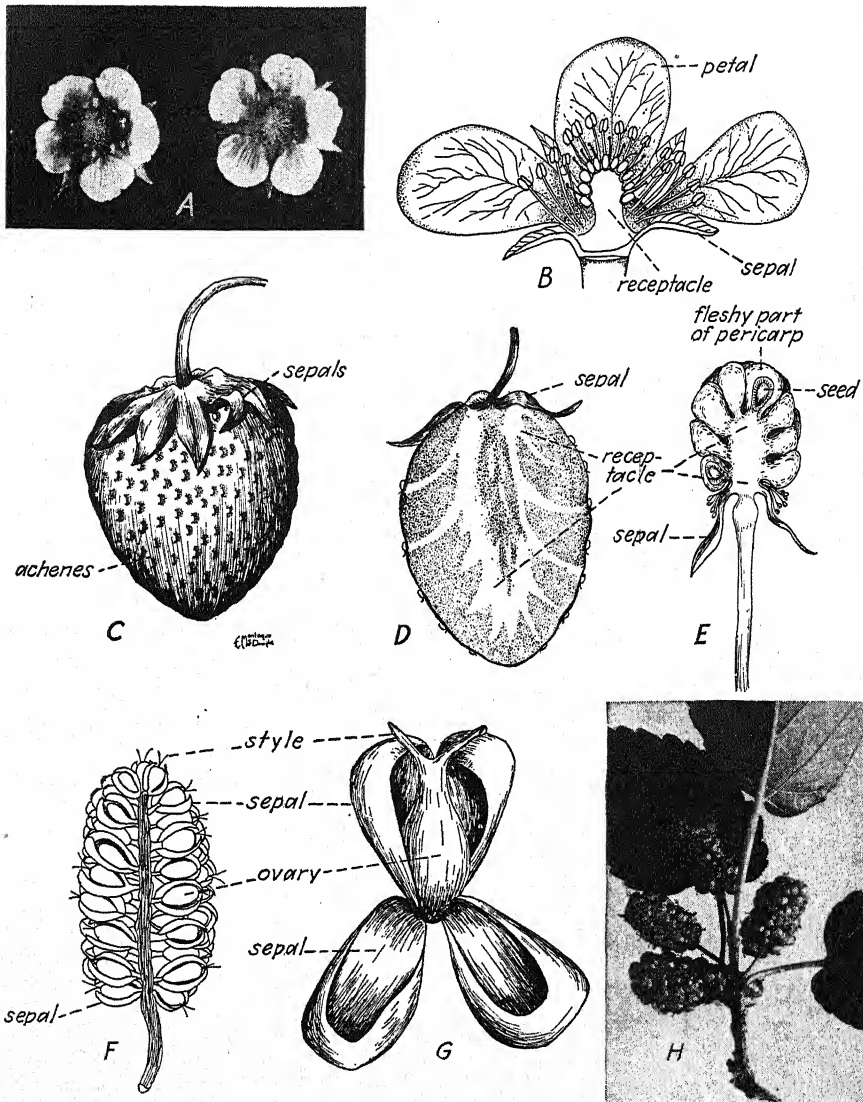


FIG. 121. Aggregate and multiple fruits; A-E, aggregate fruits; F-H, multiple fruits. A, flowers of strawberry, showing a large number of centrally located, separate pistils surrounded by a varying number of stamens; petals and sepals are both present; the arrangement of these parts is better shown in the diagram of vertical section through the flower in B; C, the mature strawberry fruit; D, the strawberry fruit cut vertically, showing the minute achenes on the surface of the receptacle tissue; E, blackberry fruit cut vertically to show structure; F, drawing of a longitudinal section through the mulberry fruit, showing structure; G, a single-pistillate flower of mulberry, showing the single pistil with two styles, surrounded by the fleshy calyx; H, photograph of mulberry fruit. (B, by Edna S. Fox; C-E, by Elsie M. McDougale; F, G, by Chris. Hildebrandt.)

as a single unit. Most aggregate fruits are fleshy. Good examples are strawberries, raspberries, and blackberries.

In the strawberry (Figs. 121, *A-D*; 314, *G*) the receptacle enlarges greatly, forming the edible part of the fruit. The true fruits of the strawberry are achenes, which are popularly thought of as seeds. In the fruit they appear scattered over the surface of the receptacle. The strawberry is also an accessory fruit.

In the raspberry and the blackberry (Fig. 121, *E*), the individual fruits are drupelets which adhere together. In the blackberry, these drupelets also adhere to the receptacle and cannot be readily separated from it. In the raspberry, the adhering drupelets can be lifted readily as a unit from the small dome-like receptacle.

In the rose fruit, commonly called a **hip**, the floral tube surrounds the matured ovaries (achenes) and becomes fleshy, the whole forming an aggregate fruit which is also an accessory fruit.

Multiple Fruits. Multiple fruits develop from entire flower clusters and thus differ from simple fruits and aggregate fruits which develop from individual flowers. In the multiple fruit, the matured ovaries of the entire flower cluster remain aggregated in a single mass. Most multiple fruits are fleshy and are also accessory fruits. Pineapples, Osage oranges, mulberries, and figs are good examples. In pineapples, the flowers are sessile on a central axis which is leafy at the apex. At maturity, the ovaries as well as axis structures are enlarged and fleshy, forming the fruit.

In the mulberry, staminate and pistillate flowers are borne in separate inflorescences, the pistillate flowers in short, dense spike-like clusters (Fig. 121, *F*, *H*). Each pistillate flower (Fig. 121, *G*) consists of four sepals (no petals) and a pistil of two carpels, only one of which develops. The two stigmas of the pistil usually persist in the fruit. At maturity, the sepals as well as parts of the one-seeded ovaries become fleshy, the entire cluster ripening as a unit.

In the fig, the upper part of the peduncle becomes fleshy and completely envelops the fruitlets, the whole structure ripening into a single multiple fruit called a **syconium**.

RÉSUMÉ OF FRUIT CLASSIFICATION

I. **Simple Fruits.** Those which are developed from a single (simple or compound) pistil, and which consist of a single matured ovary together with any accessory structures closely associated with the ovary.

A. **Dry Fruits.** Those in which the pericarp and accessory structures become more or less dry when mature.

1. **Dehiscent Fruits.** Those which split open at maturity.

a. **Legume.** Developed from a simple pistil; splitting along two sutures into two valves (peas, beans, and black locust).

(1) **Loment.** A segmented legume (tick trefoil).

- b. **Follicle.** Developed from a simple pistil; splitting along one suture (milkweed, columbine, and larkspur).
 - c. **Capsule.** Developed from a compound pistil (poppy, purslane, Iris, St.-John's-wort, and morning-glory).
 - (1) **Silique.** The elongated two-loculed capsule of the mustard family (cabbage, cardamine).
 - (2) **Silicle.** A short, broad silique (shepherd's-purse, peppergrass).
 - (3) **Pyxis.** A capsule with circumscissile dehiscence (*Portulaca*).
- 2. **Indehiscent Fruits.** Those which do not split open at maturity.
 - a. **Achene.** Small, one-seeded; seed attached to pericarp at one point only; pericarp readily separable from seed coat (sunflower, lettuce, and buckwheat).
 - b. **Grain, or Caryopsis.** Small, one-seeded; seed coat fused to pericarp over its entire surface (corn, wheat, oats, rye, and barley).
 - c. **Samara.** A winged achene (ash, maple, elm, and birch).
 - d. **Schizocarp.** Two (occasionally one) ovarian segments invested by the floral tube; the segments separate at maturity into two indehiscent mericarps (members of carrot family).
 - e. **Nut.** Pericarp hard or crustaceous throughout; usually from a compound pistil only one carpel of which develops; mostly one-seeded, usually with an involucre (chestnut, hazelnut, acorn, and beechnut).
- B. **Fleshy Fruits.** Those in which a part or all of the pericarp and any accessory structures become fleshy at maturity.
 - 1. **Pome.** Developed from a compound pistil with two or more carpels and an inferior ovary; floral tube forming major fleshy part of fruit; outer part of pericarp fleshy, endocarp cartilaginous (apple, pear, and quince).
 - 2. **Drupe, or Stone Fruit.** Mostly one-seeded fruits in which the exocarp is usually thin and skin-like, the mesocarp fleshy, and the endocarp stony (peach, plum, cherry, and olive).
 - 3. **Berry.** All parts of the pericarp fleshy or pulpy except the exocarp which is often skin-like (grape, tomato, gooseberry, and cranberry).
 - a. **Pepo.** A berry with a thick, inseparable rind (pumpkin, squash, cucumber, and melons).
 - b. **Hesperidium.** A berry with a leathery, separable rind (orange, lemon, and grapefruit).
- II. **Aggregate Fruits.** Those consisting of a number of similar small fruits (fruit-lets), all of which are developed from a single flower with many separate pistils and which mature together as a single unit on a common receptacle (together with any accessory structures) mostly fleshy (strawberry, raspberry, and blackberry).
 - A. **Hip.** The fruit of the rose, the fleshy floral tube surrounding the matured ovaries, which are achenes.
- III. **Multiple Fruits.** Those consisting of the matured ovaries of an entire flower cluster (together with any accessory structures), all adhering together in a single mass. Mostly fleshy (pineapple, mulberry, Osage orange, and fig).
 - A. **Syconium.** The multiple fruit of the fig, in which the upper part of the peduncle becomes fleshy and completely envelopes the fruits.

SEEDS

Economic Importance of Seeds. Seeds are so generally found separated from the plants that produce them and they differ so markedly in ap-

pearance from vegetative organs that we often fail to associate them with the plants producing them. In many cases, the seed or the fruit is the only part of the plant commonly known. When such plants as the pea, the bean, corn, wheat, or rice are mentioned, it is usually the seed or fruit rather than the whole plant that is visualized. This situation has resulted from the fact that, since the dawn of history, seeds have ministered greatly to the needs of man (Fig. 122). Indeed, the use of the cereals by man antedates all written historical records. In the earliest known records of the civilization of the Tigris and Euphrates valleys, man was already cultivating wheat for bread. Similarly the cultivation of rice was practiced by the ancient Chinese civilization of the valleys of the Hwang Ho and the Yangtse Kiang and the cultivation of corn by the Mayan civilization of the New World. It is significant that each of these three prominent civilizations of antiquity should have originated in a region in which one of these three cereals seems to have had its native home or to have been cultivated since prehistoric times. Barley, oats, and rye are also cereals that date back to ancient or prehistoric times. The name "cereal" itself implies antiquity, since it was given to the grains by the Romans, who derived it from the name of their goddess Ceres, the giver of grain. Even today, the cereals occupy one of the most prominent positions in the diet of man.

In addition to the cereals, coconuts, peanuts, almonds, walnuts, filberts, chestnuts, peas, beans, and lentils have been used by man as food since ancient times. While many of these are botanically fruits, it is actually the seed that serves as food.

At the present time not only are seeds the most important sources of food but they are used as drugs and in the making of beverages, medicines, paints, varnishes, clothing, ornaments, and many other commercial products. Oils are extracted from such seeds as the coconut, cotton seed, corn, flax, peanut, castor bean, soybean, and almond. These oils are used in various ways, some as food products, others in making soaps, varnishes, paints, and linoleum. Some seeds, like mustard, caraway, anise, coriander, and celery, are used as condiments. Buttons are made from vegetable ivory obtained from the seeds of a palm. Cotton, with its many uses, is the fibrous material surrounding the seeds of the cotton plant. In these and in other ways seeds are of great economic importance. Indeed, seeds are used by man more than any other part of the plant.

General Features of Seeds. The seeds of plants differ so greatly from each other in size, form, color, and other general features that the characteristics of the seed may be taken as one of the distinguishing features of a species. Even the varieties within a species can often be differentiated on the basis of their seed characteristics. In size, they vary from the dust-

like seeds of some of the orchids to the enormous seeds of the coconut. They may be spherical, ovoid, elliptic, elongated, disk-like, or very irregular in shape. The outer walls may be smooth or rough and may be

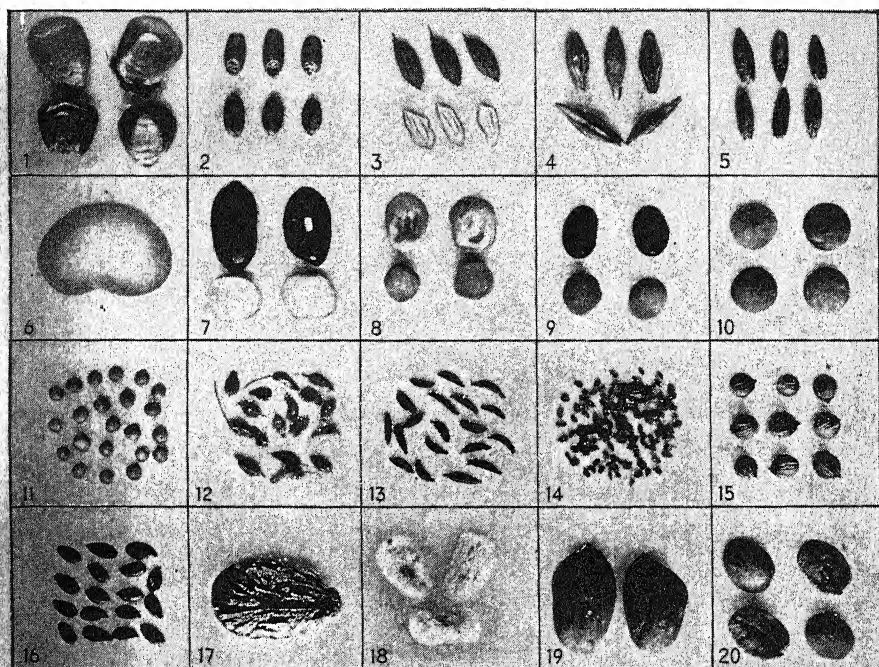


FIG. 122. Economically important seeds.

Top Row, Cereals

1, Corn (*Zea Mays*), upper two, field corn; lower two, sweet corn; 2, wheat (*Triticum sativum*); 3, rice (*Oryza sativa*); 4, barley (*Hordeum sativum*); 5, rye (*Secale cereale*). (These cereals have been used as food by man since prehistoric times.)

Second Row, Legumes

6, Lima bean (*Phaseolus lunatus*); 7, beans (*Phaseolus vulgaris*), upper two, string beans; lower two, field beans; 8, peas (*Pisum sativum*), upper two, garden peas; lower two, field peas; 9, soybeans (*Glycine soja*), upper two, variety Peking; lower two, variety Ito San; 10, lentils (*Lens esculenta*).

Third Row, Spices

11, Mustard (*Brassica alba*); 12, anise (*Pimpinella Anisum*); 13, caraway (*Carum Carui*); 14, celery (*Apium graveolens*); 15, coriander (*Coriandrum sativum*). (12-15, inclusive, are seed-like fruits, all belonging to the parsley family, Umbelliferae.)

Fourth Row, Coffee and seeds that are important sources of vegetable oils

16, Flax (*Linum usitatissimum*); 17, castor beans (*Ricinus communis*); 18, cotton (*Gossypium herbaceum*); 19, peanuts (*Arachis hypogaea*); 20, coffee (*Coffea Arabica*).

sculptured or covered with outgrowths in the form of spines, hooks, or fibers. All parts of the spectrum are represented in their colors. They may be of uniform color or mottled. Although no two species of seeds are

exactly alike in all these features, they all resemble each other in that they are ripened ovules consisting of the same general kinds of parts and in that they all serve the functions of dissemination, protection, and reproduction of the species.

GENERAL STRUCTURE OF SEEDS

The mature seed consists of one or two seed coats, an embryo, and stored food. The food may be stored in the endosperm tissue or entirely in the embryo.

The Seed Coats. The seed coats are developed from the integuments of the ovule. There are usually two of these coats, corresponding to the two integuments of the ovule, but in some ovules there is only one integument and hence only one seed coat. The outer seed coat is called the **testa**. When two seed coats are present, the inner one is often much thinner than the outer. The seed coats sometimes become very dry and hard, thereby effectively protecting the more delicate embryo within. At the place where the seed breaks off from the funiculus (now called the seedstalk) there is a scar left, called the **hilum**, and below the hilum a small pore, the **micropyle** (Fig. 123). It will be recalled that the micropyle is the former point of entrance of the pollen tube into the ovule. In seeds in which the ovule is bent over into a position parallel with that of the seedstalk, there is usually a ridge visible on the seed where the tissues of the funiculus continued on into the ovule. This ridge, now directly above the hilum, is called the **raphe**. The upper end of the raphe, where the vascular tissues spread out into the ovule, at the former junction of the nucellus, integuments, and funiculus, is called the **chalaza**.

The Embryo. Of the internal parts of the seed, the embryo is the most representative as well as the most important. It is the young plant developed from the fertilized egg and, in the mature resting seed, is always in a dormant condition. The degree to which the embryo is developed in the seed varies in different plants. Sometimes the seeds are shed from the plant before the embryo has been differentiated into well-defined parts. In such cases, further development can occur only after the seeds start to germinate. In its most advanced stage in a seed, the embryo consists of four distinct parts, *viz.*, the **plumule**, the **cotyledons**, the **hypocotyl**, and the **radicle**.

The **plumule** is in reality the first terminal bud of the embryo (Fig. 123). It may consist merely of a mass of undifferentiated meristematic tissue or, like many vegetative buds of the stem, may also have partly differentiated leaves. In any case, it gives rise to the first vegetative shoot of the plant.

The **cotyledons** (Fig. 123) are morphologically leaves, although usually they are so highly modified in shape and form as to differ markedly from

the ordinary leaves of the plant. In some cases, they are merely food-storage organs, never performing the functions of true leaves. In other cases, they are absorbing organs, and in still others they may become functioning leaves after the seed germinates. In dicotyledonous plants, as the name implies, there are two of these cotyledons, while in monocotyledons there is only one. Gymnosperms have a variable number of cotyledons. In seeds in which there is no endosperm, the food is stored chiefly in the cotyledons. In such cases, the cotyledons are usually large and fleshy and occupy most of the interior of the seed.

The *hypocotyl* (Fig. 123) is the first true stem of the plant, extending from the point of attachment of the cotyledons to the radicle. In many seeds it is the elongation of the hypocotyl that causes the cotyledons and the plumule to emerge from the seed during germination. The arrangement of the internal tissues of the hypocotyl is typically that of the stem.

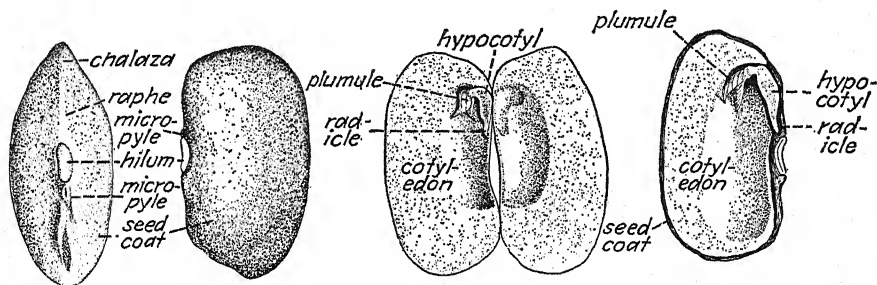


FIG. 123. Seed structure of common bean. (By Elsie M. McDougle.)

The *radicle*, or first root of the plant (Fig. 123), is located at the base of the hypocotyl. Externally the exact point of origin of the radicle cannot, as a rule, be determined in the embryo. Often it is nothing more than a mass of meristematic tissue at the tip of the hypocotyl. When differentiation has occurred, the radicle displays, internally, the typical radial arrangement of the vascular tissues that is found in roots. The tip of the radicle is always directed toward the micropyle and is the first part of the embryo to emerge from the seed during germination.

The Stored Food. The stored food of the seed may be in the form of *endosperm* or may be entirely in the embryo, chiefly in the cotyledons. When endosperm is lacking in seeds, it indicates that the embryo developed to such a stage as to absorb the endosperm completely before the seeds ripened. This condition is found in practically all legumes. In all the cereals and other grasses the food is stored largely in the endosperm tissue and is not used by the embryo until germination begins.

The foods stored in seeds consist of *carbohydrates*, *fats*, and *proteins*, the percentage of each varying greatly in different species.

The *carbohydrates* may occur as starch, hemicelluloses, or sugars, with starch predominating. Starch is always found in definite plastids, the starch grains, which have characteristic forms peculiar to a given species. In fact, the source of any particular commercial starch can be determined by the shape and form of the starch grains. Starch occurs in the cotyledons of legume seeds and in the endosperm of cereals. The cereals are especially rich in starch. Corn starch and wheat starch are familiar examples. Hemicelluloses are found in the walls of endosperm cells of such seeds as dates, coffee, and onions, making these walls very tough and hard. While hemicelluloses are used like true cellulose for strengthening cell walls, unlike cellulose, they may be digested to simpler compounds and hence may be used as reserve foods. Sugars are stored in the seeds of sweet corn and peas and in many nuts. The most common sugar found in seeds is sucrose.

Fats are found more abundantly in seeds than in any other part of the plant. Vegetable fats are obtained almost exclusively from seeds rich in stored fat. The fat usually occurs in the form of oil globules. As mentioned in a previous chapter, fats are more efficient storage foods than are carbohydrates, yielding $2\frac{1}{4}$ times as much energy per unit weight as do the carbohydrates. In the cereals most of the fat occurs in the embryo. In other plants it may be found also in the endosperm. The seeds of sunflower, flax, peanuts, soybeans, and the castor-oil plant are very rich in fats.

Proteins occur in all seeds, since they are an essential constituent of all living protoplasm, but some seeds, like the legumes, are richer in proteins than others. In the cereals the storage proteins occur in small granules called *aleurone grains*, which are found in a single layer of cells (the aleurone layer) comprising the outermost portion of the endosperm. Since proteins are important foods in the building of protoplasm, they are essential for the embryo during the germination of the seed.

SPECIFIC STRUCTURE OF REPRESENTATIVE TYPES OF SEEDS

Common Bean. The common bean (Fig. 123) may be taken as a typical dicotyledonous seed lacking endosperm. These seeds, like those of other legumes, are formed within the pod, which is the ripened ovary. Each one is attached to the inside of the pod by the funiculus or seedstalk. When the seeds are shed, the funiculus breaks off, leaving a prominent scar, the hilum. Just below the hilum can be seen the micropyle, and above the hilum is the ridge formed by the raphe. The seed coats have characteristic colors which vary with different varieties of beans but are commonly variations of brown, black, and white.

When the seeds are soaked in water, they swell considerably, and the

seed coats become soft. In this condition the seed coats are easily removed. The entire interior of the seed is occupied by the embryo and chiefly by the two fleshy cotyledons or seed leaves, which may easily be separated. On the side of the seed opposite the raphe is found the radicle, with its tip directed toward the micropyle, and continuous with it is the hypocotyl. The plumule has differentiated two well-defined leaves which fold over the growing tip. These become the first true leaves of the bean plant on germination.

In this seed and in all seeds of this type, there is no endosperm, this tissue having already been consumed by the developing embryo. Most of the food of the seed is stored in the two large cotyledons, which in this case never function as true leaves.

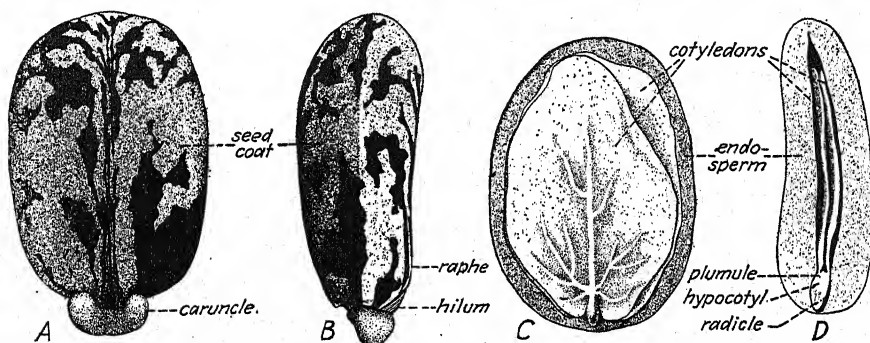


FIG. 124. Structure of castor bean seed. A, view of flat surface; B, edgewise view; C, the seed split vertically after removal of seed coats, showing the two thin cotyledons lying against the surrounding endosperm; D, the interior of the seed cut longitudinally along its narrow axis. The micropyle is concealed by the caruncle. (By Elsie M. McDougale.)

Castor Bean. Castor beans (Fig. 124) (really not beans in the ordinary sense) are produced in a capsule consisting of three carpels, each one of which bears a single seed attached by a slender stalk to the center of the base of the capsule. At maturity the capsule bursts open, forcibly ejecting the seeds. At the base of the seed is a more or less soft, spongy structure, called the **caruncle**, not commonly found on seeds. The caruncle absorbs water readily and may therefore be of some use in promoting germination. It usually obscures the micropyle. The hilum and the raphe are easily discernible. The seed coats are very hard and brittle and are often brightly colored and mottled, giving the seed some resemblance to a beetle, from which the plant received the name of *Ricinus*, which is a Latin term for a kind of insect or mite.

When the seed coats are broken away and the seed sectioned lengthwise, the interior is found to consist chiefly of a white, oily endosperm with the

embryo in the center (Fig. 124, C, D). The embryo consists of two thin leaf-like cotyledons, an entirely undifferentiated plumule, and a very short hypocotyl and radicle. This structure is typical of dicotyledonous seeds having endosperm. The endosperm of the castor bean may contain from 40 to 50 per cent of oil and 15 to 20 per cent of protein in the form of aleurone grains. It also contains a poisonous substance, ricin. The castor oil of commerce is extracted from these seeds.

Corn. The familiar corn grain (Fig. 125) is actually a fruit, since it consists of an entire ripened ovary containing a single seed. The outer hull is the pericarp, or ovary wall, fused to the seed coat. Originally there are two seed coats; but as the grain matures, the outer one disappears and the inner integument becomes flattened through pressure from within the seed. At maturity, the pericarp is so firmly fused to the remaining

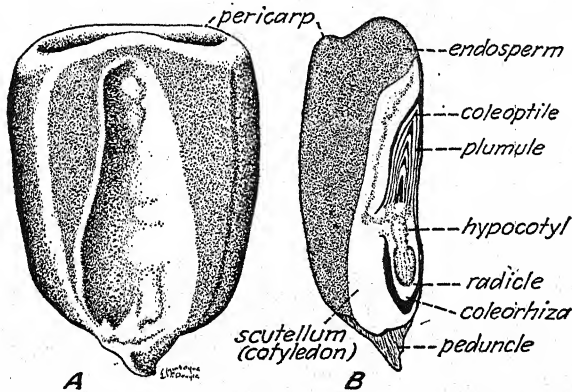


FIG. 125. The corn grain. A, view of embryo side of grain; B, longitudinal section cut at right angles to the face of the grain. (By Elsie M. McDougale.)

inner seed coat that the whole appears as a single tissue. Only by examining sections under a microscope can the actual structure be ascertained. Part of the nucellus tissue usually remains immediately inside the seed coat. The stalk-like structure at the bottom of the grain, by which it was attached to the ear, is the peduncle of the flower and fruit and not the funiculus.

The kernel is usually concave on the side of the embryo. A lengthwise section of the kernel through the center and at right angles to the broad axis (Fig. 125, B) reveals the embryo embedded in a large mass of endosperm. The outermost part of the endosperm lying next to the nucellus consists of a single layer of cells, called the **aleurone layer**, filled with aleurone grains, which are mostly protein. The remaining endosperm is often made up of two well-defined regions, an outer **horny endosperm**

and an inner **starchy endosperm**. The relative positions and the amounts of these two types of endosperm vary in different varieties of corn. The horny endosperm is of a tougher consistency and contains more protein than does the starchy endosperm.

The embryo consists of a single cotyledon, called in grains the **scutellum**, a well-developed plumule, a very short hypocotyl, and a radicle. The scutellum or cotyledon is a broad, flat absorbing organ lying against the endosperm. It never emerges from the seed, but absorbs food from the endosperm and transfers it to the growing parts of the embryo during germination. The plumule, consisting of the growing stem tip and one or more foliage leaves, is completely covered over by a sheath called the **coleoptile**. Similarly the radicle is enclosed by a sheath called the **coleorhiza**. These sheaths are characteristic of all the cereals and other grasses. The hypocotyl is extremely short and does not elongate even during germination. The whole stem of the seedling develops from the plumule or bud. In general, the structure of the corn grain is typical of monocotyledonous seeds containing endosperm.

DISSEMINATION OF SEEDS AND FRUITS

The higher plants are not able to move about but remain fixed in the place in which they grow. The fruits and seeds of these plants furnish almost the only means by which they can be spread from one place to another. One of the principal functions of the fruit is the dissemination of the seed, although the seed itself may, at maturity, possess structures that facilitate dispersal. The actual dispersal of the seeds is brought about in a great variety of ways but chiefly through the agencies of wind, water, and animals.

The wind is probably the most important agency in seed dissemination in nature. Many species of trees, like the maples, elm, birch, ash, and ailanthus have winged fruits (Fig. 126, *D-F*); others, like the trumpet creeper, catalpa, and many conifers, have winged seeds (Fig. 126, *G, H, O*) that are carried considerable distances by the wind. The hop hornbeam, the bladdernut (*Staphylea*), and other plants produce their seeds in bladder-like fruits (Fig. 126, *P*), while the black locust (Fig. 126, *A*) and honey locust have thin, dry elongated pods. Both of these types of fruits are easily blown about by the wind. Sometimes the seeds themselves, like those of many orchids, are so tiny and light as to be blown through the air like dust. In the dandelion, goldenrod, wild lettuce, asters, and other plants, tufts of hairs are found on the small, single-seeded fruits (Fig. 126, *M, U*) and act like parachutes that permit the wind to carry them great distances. It is interesting to note that some of the worst weeds and most widely spread plants have seeds or fruits

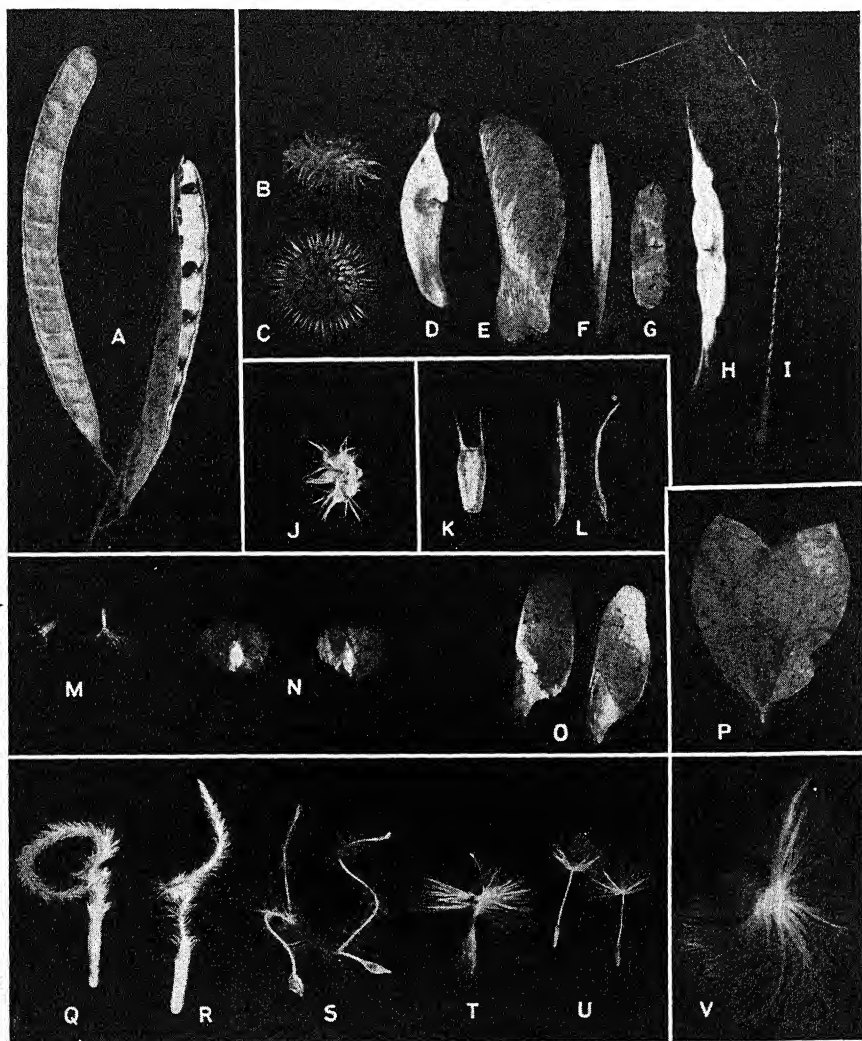


FIG. 126. Seed and fruit dispersal. A, pods of black locust; B-C, spiny fruits of cocklebur and burdock, respectively; D-F, winged fruits of tree of heaven, maple, and ash, respectively; G-H, winged seeds of trumpet creeper and of catalpa; I, fruit of the grass *Stipa* with twisted awn; J, prickly fruit of the sand bur; K, fruit of beggar tick with sharp barbs; L, fruits of sweet cicely with minute barbs; M, parachute fruit of goldenrod; N, winged fruit of birch; O, winged seeds of hemlock; P, bladder-like fruit of the bladder nut; Q-R, plumose fruits of *Erodium*; S-T, plumed fruits of *Clematis* and *Geranium*, respectively; U, parachute-like fruit of dandelion; V, plumed seed of milkweed.

that are distributed by this method. In *Clematis*, *Geranium*, and *Erodium* (Fig. 126, Q-T) the style of the flower persists on the fruit and becomes plume-like, functioning like the tufts of hairs on the fruits just mentioned. In the milkweed (Fig. 126, V) and in cotton the tufts of hairs are outgrowths from the seed itself. In the so-called "tumbleweeds," like some of the pigweeds, some grasses, and false indigo, the whole plant breaks off at the surface of the soil and, forced by the wind, rolls over the ground, distributing the seeds as it goes. The poppy, evening primrose, toadflax, and many other plants produce tiny seeds in capsules that open at the apex. When these capsules are shaken by the wind, the seeds are scattered in all directions.

Many fruits and seeds that are carried by the wind fall into streams in which they may be transported farther. This is especially true of seeds and fruits of plants growing on the banks of streams or near them. The light fruits of ragweed and of many sedges are probably carried this way. The seeds of some water lilies have buoyant coverings that enable them to float. The distribution of the coconut along the shores of tropical seas has been thought to be at least partly attributable to the buoyant, salt-water-resisting outer husk of the fruit.

Another less common method by which plants disperse seeds is by means of explosive fruits. In some of the vetches and other legumes, as the pod ripens, unequal forces and strains are set up in the tissues which finally cause the pod to burst open forcibly and scatter the seeds in all directions. After this has happened, the two valves of the pod remain curled up or twisted. The capsules of witch hazel and of the castor-oil plant forcibly eject their seeds in a somewhat similar fashion. In the "squirting cucumber" and in "touch-me-not" the seeds are ejected while the fruit is still soft and succulent. In this case, osmotic or turgor forces probably cause the explosion of the fruit.

Animals are instrumental in disseminating seeds in a variety of ways. In some cases, as in many fleshy fruits, the seeds may be passed through the digestive tract uninjured, when the fruit is eaten. Birds distribute the seeds of many berries and other fleshy fruits in this manner. Sometimes only the fleshy part of the fruit is eaten and the seeds discarded in places where they give rise to new plants. Squirrels and other animals are instrumental in disseminating such species as dogwood, hickory nuts, walnuts, and oaks by collecting the fruits and hiding them in various places. Many species of plants produce fruits or seeds that adhere to the fur or hair of animals or the clothing of man and are distributed in this way. In the so-called "beggar's-lice," in Spanish needles, in cocklebur, and in burdock, this is brought about by the hooks or barbs of the fruit (Fig 126, B, C, J-L). The grains of many of the grasses have long

awns (Fig. 126, *I*) and other structures that cause them to adhere to the wool of sheep and to other animals. The seeds of mistletoe are sticky and adhere to the feet of birds, by which they are transported from one tree to another. Many other examples of this type of dispersal might be given. It should perhaps be mentioned that the widest dissemination of useful species of plants has been brought about by man himself through his agricultural and industrial operations. At the same time he has also been instrumental in introducing many bad weeds that were present as impurities in crop seed and in other agricultural products.

VITALITY, LONGEVITY, AND DORMANCY OF SEEDS

Vitality and Longevity of Seeds. As previously stated, the seed contains an embryo in a dormant condition. Under proper conditions, this embryo is able to germinate, *i.e.*, to continue growth and thus develop into a new plant. So long as these conditions are not met, the seed may remain dormant or, if the conditions are adverse, the embryo may die. By the **vitality**, or **viability**, of the seed is meant its capacity to renew growth or germinate. By **longevity** is meant the length of time the seed can remain dormant and still be viable. Both of these are variable factors in any seed, since they are governed not only by the species of plant but also by the conditions under which the seeds were developed on the plant, as well as by the conditions to which the seeds are subjected after they are shed from the parent plant.

Seeds produced on weak, spindling plants and immature seeds are often deficient in stored food reserves and in other ways may be weakened in such a way as to reduce their vitality. When planted, such seeds usually give rise to weak plants. The temperature and other conditions under which the seeds developed on the plant also affect their vitality since they affect the physiological conditions that accompany seed development within the ovule.

Many seeds retain their vitality best under relatively dry storage conditions and under a medium to low temperature. The amount of water in the seed is closely correlated with the ability of the seed to withstand extreme temperatures. When seeds are very dry, they can be subjected to extremely low or to very high temperatures without destroying their vitality. In fact, the range of temperatures that dry seeds will withstand without injury is greater than that of any other part of the plant. Dry sugar-beet seed, for example, has been known to give 96 per cent germination after having been subjected for 30 min. to a temperature of -180°C . At the other extreme of temperature, lotus seeds have been reported to still germinate after having been subjected for 16 hr. to a temperature of $+103^{\circ}\text{C}$. Most seeds, when dry, are not injured by temperatures as low

as -10 to -20°C . It is partly for this reason that they are able to tide the plant over unfavorable conditions that would probably kill vegetative organs. It has been found that crop seeds maintain their viability best when stored under uniform conditions and preferably at a comparatively low temperature and low humidity. On the other hand, the seeds of willows, poplars, and some maples are killed if allowed to dry out. The seeds of many weeds are able to lie in the ground and be subjected to all sorts of adverse conditions, sometimes for years, without losing their vitality.

Aside from the effect of external conditions, great variation exists among different species of plants as regards the longevity of their seeds. In some cases, the seeds remain viable only a short time, no matter what the external conditions may be. In other cases, seeds retain their viability for many years. All lose their viability in time. The longest authentic case of longevity of seeds on record is that of Indian lotus seeds which were able to germinate after having been buried in a peat bed for probably more than 200 years. The longevity of most seeds is decidedly less than this, although some legumes have been known to retain their viability for 50 years and more. Seeds of black mustard, the common pigweed, shepherd's-purse, chickweed, and other weeds have been found to germinate after being buried more than 30 years in the soil. Onion seed, on the other hand, loses its viability rapidly after a single year and many seeds of garden vegetables remain viable for only 3 to 5 years even under the best conditions of storage. Willow and poplar seeds remain viable only a short time after they are formed on the plant. Unless they germinate soon after falling to the ground, they die.

The cause of the ultimate death of seeds has not yet been adequately determined, although in some cases it is thought to be the gradual denaturing of the proteins and possibly other constituents of the protoplasm of the embryo. Other chemical changes may also contribute. That it is not the gradual consumption of the stored food reserves, resulting from the continuous though feeble respiration of the seed, is proved by the fact that large food reserves often remain after the seeds have lost their viability.

Dormancy of Seeds. The seeds of some plants are able to germinate as soon as they are matured on the plant. It is not uncommon, in a very rainy season, to find sweet corn germinating in an ear that has fallen to the ground or peas and beans sprouting in the pods in which they are formed. Wheat germinates readily in the shock in rainy weather. In the majority of species, however, and especially in many wild plants, the seeds have a distinct rest period during which they fail to germinate even when supplied with the best of ordinary germinative conditions. This period of dormancy may last only until the following spring or may extend

over a period of several years. The delayed germination of such seeds may be caused by the nature of the seed coats, by the condition of the embryo, or by a combination of both of these factors. We may refer to the first of these types as **seed-coat dormancy** and to the second as **embryo dormancy**.

Seed-coat Dormancy. When the delayed germination is caused by the nature of the seed coats, it may be brought about by (1) the impermeability of the seed coat to water, (2) the impermeability of the seed coat to oxygen, or (3) the mechanical resistance of the seed coat to the expansion of the embryo and seed contents. In all of these cases, germination results when the seed coats are filed, rubbed over abrasive materials, soaked in strong sulfuric acid, broken in any other manner that will not injure the embryo, or removed altogether.

The seeds of many of the legumes, like the Kentucky coffee tree, black locust, honey locust, Judas tree, and hard seeds of clovers and alfalfa belong to the first category. It has been found that, when seeds of clovers and alfalfa are hulled by hand, 90 per cent of the seeds are hard (*i.e.*, dormant) whereas less than 20 per cent are hard when they are hulled by machinery. The machine in this case injures the seed coats sufficiently to make them permeable to water. The seeds of canna and of many other species of plants are also impermeable to water.

The best known example of a seed the coats of which are impermeable to oxygen is furnished by the common cocklebur (*Xanthium*). The spiny fruit of this plant contains two seeds, each of which has a minimum oxygen requirement for germination, the upper seed requiring more oxygen than the lower. If the seed coats are removed or if the seeds are subjected to high temperatures or to pure oxygen, they usually germinate readily. In either case, sufficient oxygen is able to reach the embryos, whereas when the seed coats are intact it is not. In nature, the lower seed, having a lower oxygen requirement, usually germinates the year after it is formed, and the upper seed the following year, germination being facilitated by frost, heat, or other conditions that gradually modify the seed coats. This type of dormancy is found also in other composites and in some grasses. It is possible that the failure of carbon dioxide to escape from the seed may also contribute to the dormancy of such seeds.

The seed coats of the seeds of water plantain (*Alisma Plantago*), of pigweed (*Amaranthus retroflexus*), and probably of many other plants permit both oxygen and water to enter the seed, but the coats are so strong that the expanding contents are often unable to break through them and hence the seeds fail to germinate. In this case, germination takes place readily when the seed coats are broken or weakened in some manner that will not injure the embryo:

Embryo Dormancy. Embryo dormancy may be caused by a very rudimentary or undeveloped embryo or by the failure of the embryo to awaken or emerge from its resting condition.

In the chapter on the flower, it was mentioned that some seeds ripen and are shed from the plant before the embryo has developed much further than the proembryo stage. In some cases, there is little development beyond the fertilized egg. When this is true, the seeds are always delayed in their germination because of the time involved during which the embryo is developing after germinative conditions have been provided. It may take several weeks or even months before the embryo is able to emerge from the seed. This type of dormancy is rather widespread through the various groups of seed plants, being found in gymnosperms (*Ginkgo* and *Gnetum*), monocotyledons (dogtooth violet, *Erythronium denscanis*, and other Liliaceae), and dicotyledons (winter aconite, *Eranthis hyemalis*; buttercup, *Ranunculus Ficaria*; and others).

Some of the most interesting cases of dormancy, as well as the most difficult to overcome, are those in which the embryos are persistently dormant. Such seeds fail to germinate even when the seed coats are removed and the seeds placed under the best ordinary germinative conditions. Germination takes place only after a series of changes, usually called "afterripening," have taken place in the embryo. To this class belong many trees, shrubs, and other wild plants as well as many cultivated species. Among the forest species may be mentioned linden, tulip poplar, ash, pines, hemlock, and other conifers, dogwood, hawthorn, and viburnums. The seeds of such fruits as apples, pears, peaches, plums, and cherries and of flowering plants like roses, holly, iris, lily of the valley, Solomon's seal, and hundreds of other species also have embryos that must be afterripened before they will germinate. In nature, afterripening sometimes occurs during the winter, allowing the seeds to germinate in spring. Often the process continues over a period of years, some germination taking place each year. This is a very efficient method of perpetuating a species and tiding it over unfavorable growth conditions.

The changes that take place during the afterripening of seeds have not been adequately worked out with many species. In the hawthorn the acidity of the cell sap of the cotyledons gradually increases as the seeds become capable of germination. This increased acidity apparently hastens the physiological processes of the embryo which are necessary for further growth.

It has been found that many seeds of this type can be made to germinate if stratified at low temperatures. A temperature range of 0 to 10°C. has been found the most effective for the majority of the species studied. By stratification is meant the placing of the seeds between layers of sand, saw-

dust, peat, or other material and keeping them moist and at a low temperature. Peat has been found to be much more effective for this purpose than any other material. Afterripening also proceeds better when the seeds are scattered through or mixed with the peat. The period of time required for afterripening of seeds during stratification varies between 1 and 6 months, depending upon the species. This method of overcoming the dormancy of embryo-dormant seeds is of considerable practical importance to nurserymen in the propagation of species with seeds of this type.

SEED GERMINATION

Conditions Necessary for Germination. The resumption of the growth of the embryo after it has been dormant in the seed is called seed germination. Even with seeds that are not dormant in the sense described in the foregoing section, certain conditions must prevail before this renewed growth will take place. Most prominent among these are a **supply of water**, a **supply of oxygen**, and a **favorable temperature**. **Light** also is necessary or at least influential in hastening the germination of some seeds while darkness is necessary for others.

Water Supply. Mature seeds usually contain 15 per cent or less water. This low water content is one of the most influential factors keeping the seeds dormant. The protoplasm and its constituents as well as the stored foods are in so concentrated a form in the resting seed as to reduce markedly the intensity of physiological activity. Before growth of the embryo can proceed, therefore, water must be absorbed. It is not necessary, however, for the seeds to be immersed in water. In fact, it is far better for them to be rather in a moist atmosphere, since covering them with water limits the oxygen supply to the seeds. Some seeds have a remarkable ability to absorb water. Often they can obtain almost as much water from an apparently dry soil as they can from pure water, an air-dry soil furnishing enough water for germination. It is this moisture-absorbing capacity of seeds that sometimes causes them to start to germinate when they are stored in a humid atmosphere. In many cases, the seed coats consist of hydrophilic colloids. The absorption of water by such coats causes them to swell and weaken, thus permitting the expanding embryo to break through them. Even in seeds with coats that do not absorb water readily or swell, the expansion of the interior of the seed through water absorption is usually great enough to cause the seed coats to burst.

The stored food reserves are most often in an insoluble form. Before they can be used by the embryo they must be rendered soluble and diffusible. The process by which this is brought about is **digestion**. This process is described in the following chapter, but it may be said here that it can proceed only when there is an abundant supply of water present.

The digestion of the foods is also necessary to provide the materials for the increased **respiration** of the seed which always occurs during germination. Thus a supply of water is of first importance to the seed in germination. In fact, the swelling of the seed resulting from water absorption is the first indication that germination is taking place.

Oxygen Supply. Even in its most quiescent state, a seed carries on respiration. The respiration, however, in the dormant seed is usually so feeble as to be hardly detectable. Respiration is the oxidation of food as an immediate source of energy to maintain life. When the embryo resumes its growth, much more energy is needed and hence respiration increases. For this increased respiration a supply of oxygen is necessary. In many seeds the seed coats must imbibe water before they permit oxygen to diffuse through them readily, but as previously mentioned this does not mean that the seeds must be immersed in water. A few kinds of seeds are known to be able to germinate in the total absence of oxygen, but few seeds are able to complete the germination process under these conditions.

Favorable Temperature. The temperature that is required by seeds for germination varies with different kinds of seed. Each kind has a range of temperatures within which the seeds will germinate. The lowest temperature of this range is called the minimum, the best temperature the optimum, and the highest temperature the maximum. These three temperatures are called the cardinal points of temperature. The cardinal points of temperature for germination are not absolutely fixed for a species but fluctuate with different samples of the same species because of the great differences resulting from conditions under which the seeds were formed on the plant or stored. Most seeds fail to germinate at a temperature as low as 0 to 5°C. or as high as 45 to 48°C. The optimum for many seeds is between 25 and 30°C. There is so much difference in different kinds of seeds, however, that these figures have a very limited application. The best temperature for germination must be determined for each kind of seed. The effect of temperature is primarily on the physiological processes going on within the seed during germination.

Light. Light is probably of greater importance in seed germination than has heretofore been supposed. The German investigator Kinzel, who has studied for many years the influence of light on seed germination, has found that, of 964 species of plants studied, the seeds of 672 were favored by light, 258 were inhibited, and 35 were indifferent. A wide range of plants was included in this study. It is interesting to note that a large majority of the seeds (70 per cent) was favored by light. Among these are many grasses, evening primrose (*Oenothera biennis*), yellow dock (*Rumex crispus*), common mullein (*Verbascum Thapsus*), loosestrife (*Lythrum Salicaria*), and the Chinese lantern plant (*Physalis Franchetti*).

The mistletoe (*Viscum album*) and a few others will not germinate at all in the absence of light.

Light interferes with the germination of seeds of several species of *Phacelia*, chive garlic (*Allium Schoenoprasum*) and other Liliaceae, fennel flower (*Nigella sativa*), several members of the pigweed family, and with the Jimson weed (*Datura stramonium*). The small grains, corn, and many legumes such as beans and clover germinate as well in light as in darkness.

It has been found that certain conditions may partly or entirely displace the effect of light in light-sensitive seeds. These vary with different species, but among them may be mentioned removal or injury of the seed coats, keeping the seeds in an atmosphere of pure oxygen, treatment of the seeds with acids and other chemicals, especially nitrogen compounds, intermittent temperatures or high constant temperatures, and after-ripening in dry storage. Some of these are effective with one type of seed and some with another.

While many theories have been proposed to explain the effect of light on the germination of light-sensitive seeds, no adequate proof of any theory is as yet available.

Activities Accompanying Germination. When all of the necessary conditions for germination have been supplied, the seed may start to sprout. To supply these conditions we usually place the seeds in moist soil or in a suitable germinator. The first visible indication of germination is usually the swelling of the seeds and often the softening of the seed coats through absorption of water. In seeds with hard seed coats, the size of the seed may not change until the swelling of the interior of the seed bursts the seed coats. After the seeds have imbibed water, greatly increased physiological activity develops within them. By means of enzymes, the stored foods are digested to soluble and diffusible substances and thus put into a form that can be assimilated by the embryo. Respiration increases markedly, as can be shown by the heat generated and by the elimination of large quantities of carbon dioxide by the seed. The embryo itself increases greatly in size through absorption of water, and the protoplasm of its living cells becomes more dilute and therefore capable of renewed physiological activity. Through the transfer of the digested foods to the growing points of the radicle and the plumule, these organs begin to grow. The radicle usually starts its growth first and is the first part of the embryo to emerge from the seed. In some seeds, like the bean, the hypocotyl as a whole greatly elongates, carrying the cotyledons and the plumule with it out of the seed, after the radicle has emerged (Fig. 127). In others, like the pea, the hypocotyl does not elongate but the plumule itself elongates, leaving the cotyledons, still surrounded by the seed coats, in the soil (Fig. 128). In seeds containing endosperm, the stored foods

are digested and transferred to the cotyledons of the embryo and from them to the radicle and the plumule. In the grasses, the single cotyledon remains attached to the endosperm as an absorbing organ, and only the plumule and radicle elongate. In this instance, the cotyledon remains permanently beneath the soil.

Much of the increase in size of the embryo results from expansion of cells already present. The whole embryo of the seed consists of undifferentiated or only partially differentiated cells. Complete differentiation proceeds with germination. At the growing tips of the radicle and the plumule cell division takes place. The growth of the embryo therefore results from both cell division and cell enlargement. As a result of this activity, the radicle becomes a functioning root, the plumule a functioning vegetative shoot producing stem and leaves, and the whole embryo develops into a seedling. The hypocotyl, when it enlarges, produces the first functioning stem. A seed is said to have germinated when the radicle has emerged from the seed coat, but germination is usually considered complete only when the seedling has become an independent plant. The time required for the completion of germination varies greatly with different species. Seeds like mustard or radish will often begin to germinate within a day and complete the process in a week or less. Other seeds may require a much longer period. In the case of seeds with very rudimentary embryos many weeks may elapse before the embryo emerges from the seed coats.

SEEDLINGS

As previously stated, the seedling is the young plant that has just emerged from the seed during germination, having developed from the renewed growth of the embryo. The seedling stage of the plant lasts from the time the embryo emerges from the seed until it becomes independent of the stored food reserves of the seed. Seedlings are of several types, depending upon the manner in which the cotyledons function during germination. Figures 127 to 129 illustrate the different types.

In the common bean (Fig. 127), the food is stored largely in the cotyledons. After digestion, it is translocated to the hypocotyl, the radicle, and the plumule. The radicle emerges first, after which the hypocotyl elongates rather rapidly, carrying with it the two cotyledons and the plumule. Under the stimulus of gravity, the radicle bends downward into the soil, while the hypocotyl elongates in the opposite direction. Many root hairs are formed on the radicle and secondary roots begin to develop almost immediately. Together they tend to hold the seedling in position. At first there is a distinct bend in the hypocotyl, but as germination proceeds it straightens out and the two cotyledons spread

apart so as to occupy opposite positions on the hypocotyl. During this time, the plumule develops rapidly and differentiates the two first functioning foliage leaves. The cotyledons often develop chlorophyll and thus carry on photosynthesis for a while, but they never assume the shape and form of true leaves. The food that is stored in them is gradually digested and transferred to the growing parts of the young plant where

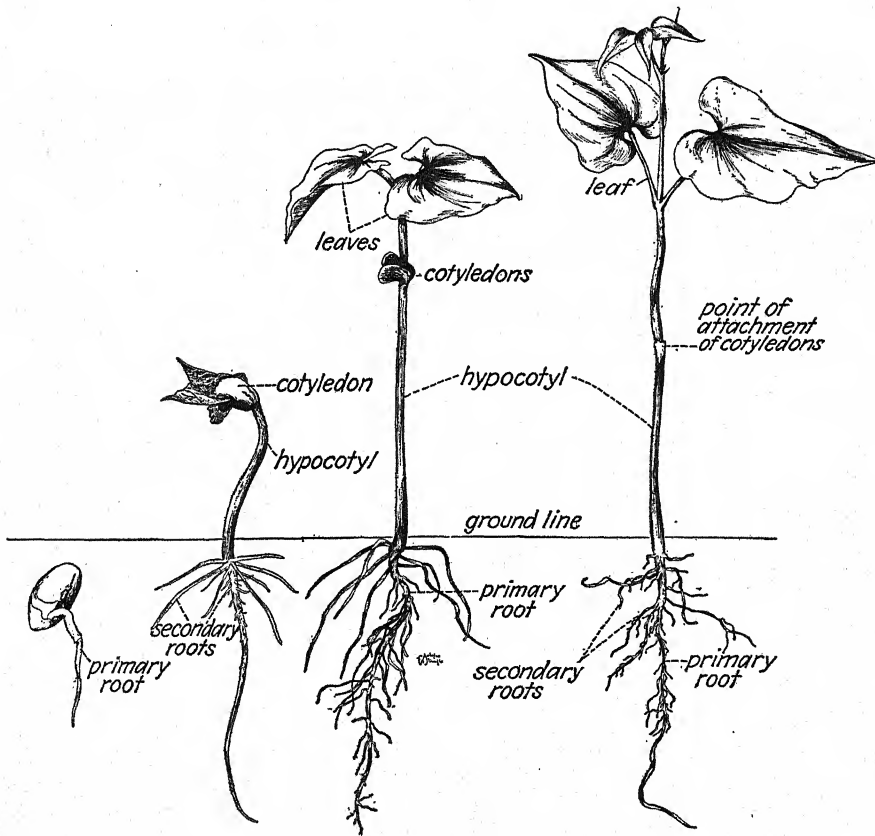


FIG. 127. Stages in germination of bean seed and establishment of seedling. (By Elsie M. McDougale.)

it is consumed. Finally they shrivel up and fall off. By this time the plumule has become an actively growing vegetative shoot, the hypocotyl a functioning stem, and the radicle a root with many branches. In this stage the seedling is an independent plant. In the bean, as in practically all other dicotyledonous plants, the first two foliage leaves formed are entirely different in shape and form from those later formed. In common

with other plants having compound leaves when mature, the first two leaves of the bean are simple.

In the pea (Fig. 128), the hypocotyl never elongates and therefore the cotyledons remain underground. The radicle emerges first, as in the bean, but the plumule develops much more rapidly, giving rise to the first true

stem of the plant as well as to the leaves. The cotyledons finally disintegrate as the food in them is consumed by the developing seedling.

The germination of the castor bean (Fig. 129, A) is somewhat similar to that of the bean except that the cotyledons are relatively thin structures that function first as absorbing organs and later as true leaves. The endosperm of this seed is carried up with the cotyledons as the hypocotyl elongates. The cotyledons do not spread apart entirely until the endosperm has been almost entirely consumed. When they finally do separate, the remaining endosperm dries up and falls off. Often remains of the endosperm and of the broken seed coats adhere for a while to the cotyledons. The plumule of the castor bean requires considerable time to get under way, since it is hardly more than a mass of undifferentiated cells in the seed. The cotyledons become green and function as foliage leaves for

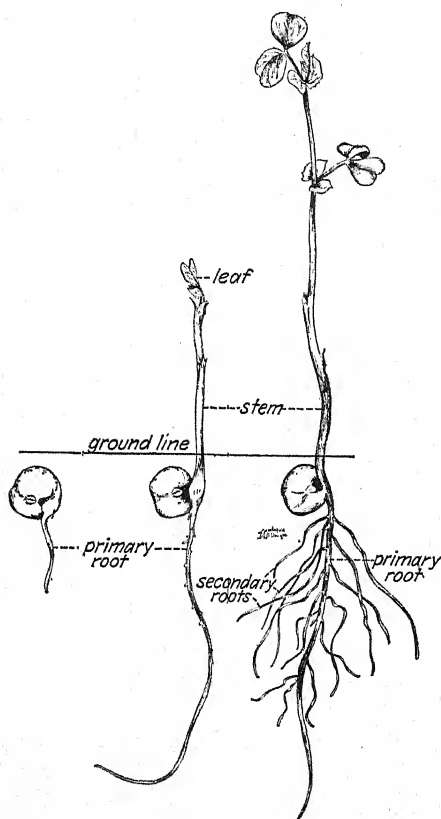


FIG. 128. Stages in germination of pea seed and establishment of seedling. (By Elsie M. McDougale.)

a long time. This method of germination is characteristic of dicotyledonous seeds having endosperm.

The germination of corn (Fig. 129, B) may be taken as typical of all cereals and other grasses. In this case, there is only one cotyledon, the scutellum, and it functions exclusively in absorbing the digested food from the endosperm and transferring it to the growing parts. All growth of the seedling results from the elongation of the radicle and of the plumule. The hypo-

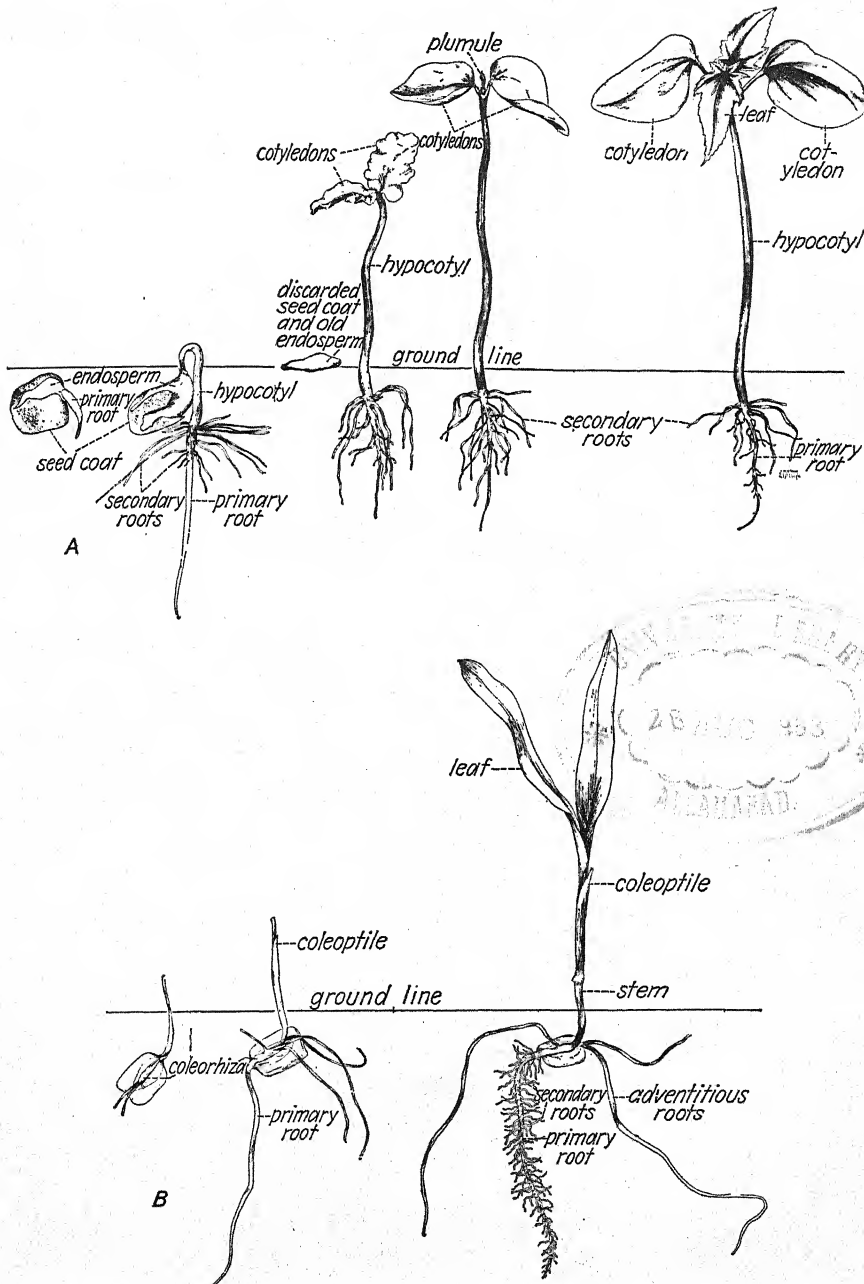


FIG. 129. Stages in the germination and establishment of seedlings of castor bean and corn; A, castor bean; cotyledons develop into green leaves; B, corn. (By Elsie McDougle.)

cotyl, as in the pea, does not elongate. The radicle emerges first but is followed almost immediately by the plumule. The radicle gradually breaks through the coleorhiza and forms the primary root. Adventitious roots begin to develop at once from the point of origin of the radicle on the hypocotyl. These adventitious roots develop very rapidly, forming a rather extensive fibrous root system. The primary root is usually of short duration. Later, adventitious roots also develop at the first nodes of the stem. The coleoptile keeps pace with the growth of the plumule for some time but is ultimately broken through as the first true leaves emerge. When germination is complete and the seedling has become independent of the endosperm, what is left of the seed gradually decays in the soil.

There appears to be a correlation between the functioning of the cotyledons as leaves and the rapidity of development of the plumule. In plants such as the bean and pea, the cotyledons do not function as leaves. In these cases the plumule develops rapidly, forming true leaves. In plants like the castor bean and the buckwheat, the embryo of the seed has cotyledons which function as leaves. In these the plumule development is delayed to a considerable extent.

CHAPTER 12

METABOLISM—THE CATABOLIC PHASE DIGESTION—RESPIRATION—FERMENTATION

The anabolic phase of metabolism was taken up in Chap. 5. It will be recalled that the anabolic phase of metabolism consists of building-up, or synthetic, processes. The catabolic phase, which is the subject of the present chapter, consists of tearing-down processes. The principal catabolic processes are digestion, respiration, and fermentation. Both phases are essential to the proper physiological balance of the plant, which culminates in assimilation and growth and which keeps the plant in a healthy, living condition. It should be kept in mind that the ability to carry on metabolism as a whole is one of the fundamental properties of protoplasm and hence metabolism takes place in every living cell. Metabolic processes, however, reach their highest intensity in actively growing regions of the plant. Since the embryos of germinating seeds are in an active state of growth, they furnish excellent material for studying such processes as digestion and respiration. It is partly for this reason that the discussion of the catabolic phase of metabolism has been postponed until germination has been considered.

DIGESTION

Introduction. In Chap. 5, an attempt was made to show how the plant synthesizes the foods needed for its existence. These foods are always made within living cells. Not all of the living cells of the plant are capable of synthesizing all the foods they need to maintain life. Carbohydrates, for example, can be synthesized only in cells containing chloroplasts. In order that cells lacking chloroplasts, such as the cells of the root, may be supplied with carbohydrates, it is necessary for carbohydrates to be transported to them from the chlorophyll-containing cells. But in order that this may be accomplished, it is necessary that these foods pass through living protoplasmic membranes. As has already been mentioned, in most of the dicotyledons, carbohydrates are temporarily stored in the cells of the leaf mesophyll in the form of starch. Starch, being insoluble in water, is incapable of passing through a protoplasmic membrane. Hence, it must first be changed to a soluble compound before it can be moved out of the mesophyll cells.

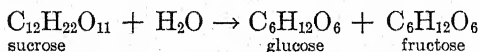
Similarly, when starch is stored in roots, in stems, or in any other organ

of the plant, it must first be changed before it can be utilized by the plant. The same may be said of fats and proteins. Not only must these foods be rendered transportable but they must be put into such form that they can be oxidized for their stored energy (respiration) or utilized in the building up of other organic substances and protoplasm. *The processes involved in rendering foods soluble and diffusible so that they may be transported or utilized in the general metabolism of the plant are collectively called digestion.*

Seat of Digestion in Plants. In the higher animals, including man, primary digestion of food takes place in a definite set of organs known as the digestive tract from which the digested products are passed into an elaborate circulatory system extending to all parts of the body. There is nothing comparable with this in plants. No specific set of organs is set aside for digestion. The process occurs chiefly in the parts of the plant where foods are stored, although it may occur in any living cell. Digestion of stored food occurs very rapidly in germinating seeds and in tubers and roots renewing growth in spring. At such times large amounts of food are necessary for the construction of new cells and for the energy required in the rapid metabolism occurring in the growing regions.

Digestion in plants is sometimes classified as **intracellular** and **extracellular**. **Intracellular** digestion occurs inside the cell. It is found to take place especially in cells containing food reserves, such as those which occur in storage roots and tubers and in seeds. Intracellular digestion also takes place in the mesophyll cells of the leaf. When the foods are digested outside the cell and the digested products absorbed by the cell, the digestion is said to be **extracellular**. This type of digestion occurs in insectivorous plants, such as the pitcher plants and sundew. The insects that are trapped by these plants are usually digested on the outer surface of the leaf and the digested product absorbed. Extracellular digestion is the common form used by the fungi.

General Nature of Digestion. Chemically, all digestion is **hydrolysis**, *i.e.*, it involves a change or splitting of compounds into simpler compounds by the chemical addition of water. This change may be illustrated by the digestion of cane sugar (sucrose) as follows:



Hydrolysis does not result in a complete decomposition of foods with release of all their energy but simply transforms them into more soluble or available forms. The combined end products still retain almost as much energy as the original substance hydrolyzed. Thus the heat of combustion of a gram-molecular weight¹ of sucrose is 1,349,600 cal., while

¹ A gram-molecular weight equals a molecular weight in grams.

the heat of combustion of the glucose and fructose resulting from the hydrolysis of the sucrose is 1,348,600 cal.

Hydrolysis of this type implies an abundant supply of water, but if the foods, in a pure state, were simply mixed with water the process would go on at an extremely slow rate. The rate is tremendously increased in both plants and animals by the action of organic catalysts called **enzymes**. Enzymes are so essential to digestion that some knowledge of them is necessary before the digestive processes can be understood.

Enzymes. Enzymes have been defined as catalysts produced by living organisms. A **catalyst** is a substance which is capable of accelerating the rate of a chemical reaction by its presence. Catalysts usually are found unchanged after the reaction is completed and hence are able to bring about almost unlimited chemical change without themselves being used up, although their action is usually checked by the accumulation of the end products of the reaction. As an example of the action of a simple inorganic catalyst may be mentioned the preparation of oxygen gas from potassium chlorate. When potassium chlorate is heated, it very slowly gives off oxygen; but if a little manganese dioxide is mixed with it, the gas is evolved very rapidly. The manganese dioxide, while greatly accelerating the reaction, can be recovered unchanged when the reaction is completed. In other words, the manganese dioxide acts as a catalyst.

Enzymes, likewise, accelerate chemical reactions without appearing chemically combined with one of the end products when the reaction is completed. Enzymes, however, differ in many ways from inorganic catalysts. To begin with, they are very sensitive to temperature. Low temperatures check their action but do not destroy them. A temperature of 100°C. is high enough to destroy most enzymes completely, and many of them are entirely inactivated at a temperature of 70°C. Enzymes, furthermore, are colloidal substances that ordinarily do not pass through parchment membranes. They are sometimes prepared by precipitation from water extracts of plant or animal tissues in which they occur. Being colloidal, they carry down on precipitation, by adsorption (*i.e.*, by a close physical union), some of the constituents of the solutions from which they are prepared. In recent years many enzymes have been obtained in a pure, crystalline state (Fig. 130). Among these are *urease*, *pepsin*, *trypsin*, *papain*, *tyrosinase*, *catalase*, *peroxidase*, and *ascorbic acid oxidase*. All enzymes thus far isolated have been found to be proteins.

One of the most interesting features about enzymes is the fact that they are specific in their action. The enzyme *urease*, for instance, acts on urea and nothing else. *Catalase*, an enzyme of wide distribution in plants and animals, accelerates the decomposition of hydrogen peroxide to free oxygen and water but has no effect on other compounds. Similarly, most enzymes accelerate only a particular chemical reaction and have no effect

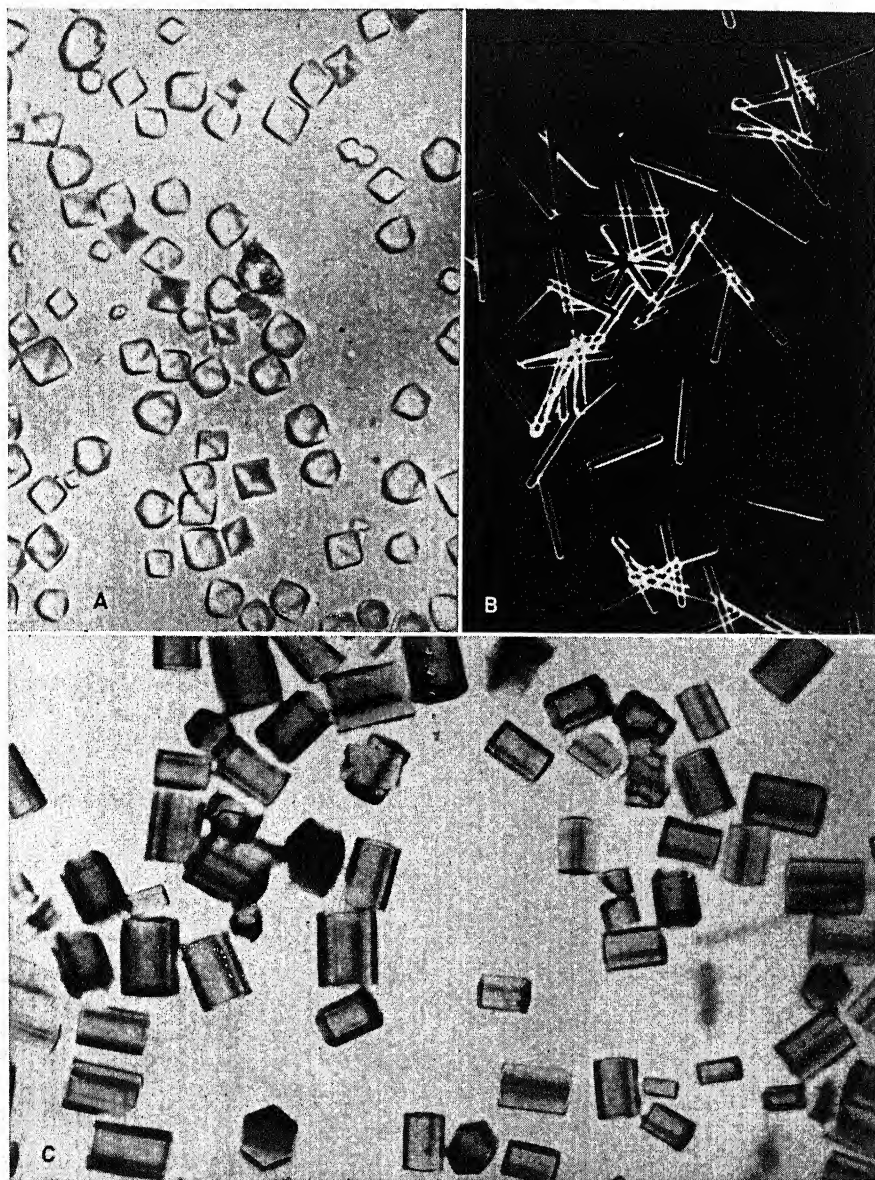


FIG. 130. Crystallized enzymes; A, urease, the first enzyme ever to be prepared in crystalline form; B, trypsin; C, catalase (from beef erythrocytes). (From photomicrographs furnished by Dr. James B. Sumner, Laboratory of Enzyme Chemistry, Cornell University, Ithaca, N.Y. Dr. Sumner was the first to prepare any enzyme in pure crystalline form.)

on other reactions. On the other hand, many of the enzymes are capable of causing a reaction to take place in either direction. For example, *lipase*, under certain conditions, causes the hydrolysis of fats to fatty acids and glycerol but under other conditions may bring about the condensation of fatty acids and glycerol to fats.

Among the factors which affect the rate of activity of enzymes may be mentioned temperature, concentration of the substrate, concentration of the enzyme, accumulation of end products of the reactions, the acidity or alkalinity of the medium, light, and the presence of certain substances which may act as accelerators or paralyzers of enzyme action. Salts of the heavy metals such as silver nitrate, mercuric chloride, and copper chloride retard the action of many enzymes. Most enzymes are sensitive to the reaction of the medium in which they occur, some requiring a slight acidity and others a slight alkalinity for optimum activity. Light, and especially ultraviolet radiation, may destroy some enzymes or modify their activity. The catalytic activities of many enzymes depend not only upon the chemical make-up of the basic part of the enzymes but also upon the presence of certain substances which combine specifically with the enzymes. These may be simple inorganic substances or complex organic substances, and are called **prosthetic groups**, or **coenzymes**. Thus copper acts as the prosthetic group of *ascorbic acid oxidase*, an enzyme which catalyzes the oxidation of ascorbic acid (vitamin C); magnesium forms the prosthetic group for the action of *phosphatases* or *phosphorylases* in liberating or transferring phosphate groups; *coccarboxylase*, which is the pyrophosphate ester of thiamin (vitamin B₁), is the coenzyme of *carboxylase*. Coenzymes have been found associated chiefly with oxidizing enzymes. Thus far hydrolytic enzymes, like the majority concerned in digestion, have been found to have no prosthetic groups. With enzymes requiring coenzymes for their action, the part of the enzyme without the coenzyme, which, in most cases, is the protein part of the enzyme, is sometimes called the **apoenzyme**; and the intact enzyme, consisting of apoenzyme and coenzyme, is referred to as the **holoenzyme**.

Enzymes are named either according to the type of substance upon which they act or according to the type of reaction they accelerate. Thus enzymes that catalyze the splitting of carbohydrates are called *carbohydrases*. Similarly, the ending *-ase* is substituted for the ordinary ending of any other substrate upon which a particular enzyme acts, and this name given to the enzyme. The enzymes *sucrase*, *cellulase*, and *amylase* were named in this way. Enzymes which cause hydrolysis are called *hydrolases*; those which cause oxidation are called *oxidases*, and so on. Many of the enzymes were known before this system of naming enzymes was adopted. The names of such enzymes were not changed under the

new system. In this category belong *pepsin*, *trypsin*, *bromelin*, and many other enzymes.

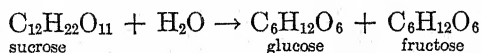
Most of our knowledge of enzymes and hence of digestion has been obtained from *in vitro* studies. When we consider the complex chemical environment of enzymes occurring within living cells of the plant, it is not remarkable that our knowledge of the precise mechanism of digestion of any substance within the plant is far from complete and that many of the conclusions which are now considered to be correct will probably be modified in the future.

It should be mentioned that enzymes are important not only in digestion but also in practically all the metabolic processes that take place in the plant.

Digestion of Carbohydrates. Of the carbohydrates found in plants, glucose, fructose, sucrose, starch, cellulose, and hemicelluloses occur in greatest abundance. Of these, glucose and fructose are the simplest, being monosaccharides. These two sugars are soluble, diffusible, and in a form capable of being used directly in the metabolism of the plant. Hence they require no further digestion. In fact, they are the most common end products of the digestion of other carbohydrates. Sucrose, starch, cellulose, and hemicelluloses must first be digested before they can be utilized.

Sucrose Digestion. As mentioned in a previous chapter, sucrose, $C_{12}H_{22}O_{11}$, or cane sugar, is the most widely distributed disaccharide found in plants. It is a common storage carbohydrate in many monocotyledonous plants like sugar cane and occurs also in the stems, roots, leaves, and fruits of many of the dicotyledons. Being readily soluble in water, it is ordinarily diffusible, but some plant-cell membranes are impermeable to it. Sucrose as such is nonfermentable. The advantage to the plant in having it digested may rest on the probability that it cannot always be used directly in respiration or assimilation or in the synthesis of other organic substances.

The digestion of sucrose yields glucose and fructose according to the following equation:



This reaction is accelerated by the enzyme *saccharase* (also called *invertase*, *sucrase*, or β -*h-fructosidase*). This enzyme has been found to occur in green leaves, fruits, grains, stems, potato tubers, some roots, pollen, and such lower plants as fungi and bacteria. It is especially abundant in yeast. Salts of the heavy metals (silver, copper, mercury) inhibit its action. Maximum activity is obtained with low concentrations of

sucrose (5 to 10 per cent). *Saccharase* also hydrolyzes the sugars raffinose, gentianose, and stachyose and, to some extent, inulin.

Starch Digestion. Starch is the most common storage form of carbohydrate found in plants. Being insoluble in water, it must always be changed before it can be used or transported. It is always found in the plant in the form of grains, the starch grains, which vary in form in different species. Starch grains usually contain, in addition to starch, less than 1 per cent of adsorbed other substances, including fats, proteins, tannins, phosphates and other minerals, and hemicellulose. The starch exists in the grains in colloidal condition, probably as colloidal aggregates of starch molecules in some way bound up with phosphates. Chemically, starch consists entirely of glucose units. Most natural starches are made up of at least two chemically different components, *viz.*, **amylose**, consisting of a linear, unbranched chain of glucose units, and **amylopectin**, which is a branched chain of glucose units. The proportions of these two components apparently differ widely in starches of different plants. Some starches contain 10 to 20 per cent or more amylose and 80 to 90 per cent or less amylopectin.

The enzyme complex concerned in the digestion of starch is commonly called *diastase*. *Diastase* is found widely distributed in plants. It is found in the majority of seeds and leaves, in the juices of roots and tubers, in fruits, in wood and bark of trees, in germinating pollen, in the latex of rubber trees and poppies, and in some of the fungi. The seeds of legumes and cereals are especially rich in *diastase*. The amount of *diastase* increases greatly during the germination of starchy seeds, where the digestion of starch proceeds rapidly. A young seedling may have a *diastase* content one thousand times greater than that of the seed from which it grew. The maximum *diastase* content is usually reached at the time of the formation of the first leaves of the seedling. In barley, this occurs about 11 or 12 days after the beginning of germination.

Malt diastase is one of the most common forms used in experiments on starch digestion. It is prepared from germinating barley grains in various ways, usually by extracting with water and precipitating several times with alcohol. *Takadiastase*, a form commonly used in medicine, is prepared by growing the fungus *Aspergillus Oryzae* on steamed bran or rice for 40 to 48 hours and then extracting the enzyme with water and precipitating with alcohol.

Diastase is not a single enzyme but consists of several separate enzymes with different properties. How many of these separate enzymes may be present in a *diastase* preparation has not yet been determined, but prominent among them are the *amylases* (so named from the Latin *amylum*, which means starch), including the dextrinogenic (dextrin-forming) α -*amylase*

and the saccharogenic (sugar-forming) β -*amylase*. There may also be present *phosphatase* such as the starch-liquefying *amylophosphatase*, which has been reported to be able to break down the colloidal structure of the starch, and *phosphorylases*, which have been shown to function in the synthesis of starch out of sugars. *Maltase*, an enzyme which hydrolyzes maltose to glucose, is also usually found in tissues containing diastase.

In general, starch is ultimately broken down in digestion in the plant, to glucose, with the intermediate production of, possibly, soluble starch, various dextrans, and maltose. A number of different enzymes of the *diastase* complex are involved. Starch may be converted first into soluble starch by the action of *amylophosphatase*, although the presence of this enzyme has not been fully established.

The action of β -*amylase* consists of the progressive removal of maltose units from the ends of chains of glucose molecules. The unbranched component of starch, amylose, is completely hydrolyzed by β -*amylase* to maltose. The branched component, amylopectin, on the other hand, is converted to maltose to the extent of only about 50 per cent, the residue being a relatively long-chain dextrin, called dextrin A or α -amylodextrin. The incompleteness of the hydrolysis of amylopectin by β -*amylase* is ascribed to the presence of the cross-linkages in the amylopectin. These cross-linkages, or points of branching of the chains of glucose molecules, in amylopectin are thought to interfere with the further action of the enzyme. When β -*amylase* acts directly on starch, which contains both amylose and amylopectin, about 60 per cent of the starch is converted to maltose, the remaining residue being α -amylodextrin, which still gives a blue-violet color with iodine.

The action of α -*amylase* is somewhat more complex than that of β -*amylase*. In the early stages of its reaction it produces only short-chain dextrans but no maltose. The short-chain dextrans are called reducing dextrans because they reduce Fehling's solution. They give no iodine reaction. In later stages of reaction of α -*amylase*, the dextrans themselves may be hydrolyzed with the production of maltose and perhaps some glucose. As a result of the action of the *amylases*, maltose tends to accumulate, but if *maltase* is present, it converts the maltose to glucose, maltose being made up of two molecules of glucose. In the plant the glucose resulting from starch digestion may immediately be converted into fructose or sucrose. Maltose and dextrans are found rarely and in small amounts in plants.

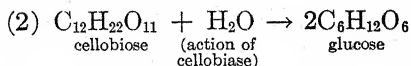
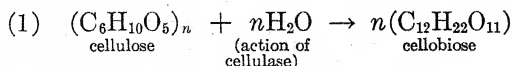
The digestion of starch can best be studied by using a starch paste made up by mixing a gram of starch with a little water and stirring it into 200 cc. of boiling water and allowing to cool. When starch grains are used, the action of *amylases* is very slow, often causing localized corrosion of the grains and resulting in an empty hull after

digestion is complete, due to an outer layer of the grains, which may be a less hydrated form of starch. When a starch paste is made, action is more rapid. If the digestion is studied by means of iodine tests, color changes occur from blue through violet, red, and red-brown to colorless. These changes are associated with the production of definite fragments of the starch molecule, which are dextrins and maltose. Fragments containing 6 units or less of glucose give no color reaction with iodine; those containing 8 to 12 units give a reddish coloration, and those containing 12 units or more give a violet to blue reaction. The different kinds of dextrins are simply fragments of the basic starch molecule, consisting of 3, 4, 8, 12, or possibly 16 to 17 glucose units. At the end of the reaction, the presence of reducing substances, mostly maltose, can be detected with Fehling's solution.

Digestion of Cellulose and Hemicellulose. Celluloses and hemicelluloses are both found in the walls of the cells of plants. Cellulose is chiefly a structural material, but the hemicelluloses may sometimes be used as reserve food.

The enzymes concerned in the digestion of cellulose have been isolated chiefly from bacteria and fungi that cause decay. It is these organisms which break down the relatively insoluble celluloses in plant remains in the soil and in decaying timber.

Cellulose is hydrolyzed by the enzyme *cellulase* to a disaccharide called cellobiose. The enzyme *cellobiase* then converts the cellobiose into 2 molecules of glucose. This may be represented as follows:



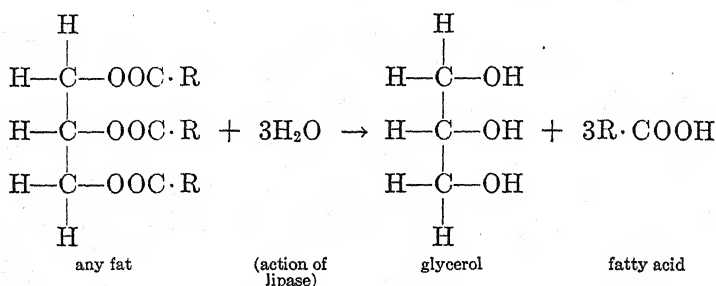
The exact mechanism of the digestion of cellulose has not been as thoroughly determined as has the digestion of other carbohydrates. It is likely that it is much more complex than is indicated by the two equations above and that other enzymes are involved.

The digestion of the hemicelluloses is brought about by enzymes called *cytases* and results in such end products as glucose, mannose, galactose, and pentoses.

Digestion of Fats and Oils. The digestion of fats and oils can best be observed in the germination of fatty seeds in which relatively high percentages of fat occur. It has been mentioned in a previous chapter that fats are esters of glycerol and fatty acids. Before a fat can be utilized by the plant or translocated to some other region, it must first be rendered soluble and diffusible. This is brought about by a class of enzymes known as *esterases* because they accelerate the hydrolysis of esters. Of the different kinds of esterases found in plants, only *lipase* need be considered here.

Plant *lipase* has been isolated chiefly from germinating seeds, such as castor beans and the seeds of other members of the spurge family (Euphorbiaceae), soybeans, seeds of cucurbits, flax, hemp, rape, poppy, and corn. *Lipase*, it will be recalled, is the same enzyme that causes the synthesis of fats from glycerol and fatty acids. Whether it causes synthesis or hydrolysis is at least partly governed by the relative water content of the tissue in which it occurs. When the water content is diminishing, as when seeds are being formed on the plant, synthesis of fats occurs. When the water content is increasing, as when seeds are placed under germinating conditions, *lipase* hydrolyzes the fats that are present. It is for this reason that the acid content of fatty seeds increases during germination. The hydrolysis proceeds very slowly at first, but as the percentage of acid formed increases, the rate increases. In other words, a little acid accelerates the action of *lipase*.

The digestion of the fat may be represented as follows:



If palmitic acid were the fatty acid involved in the above reaction, R would be $\text{C}_{15}\text{H}_{31}$ in each case. Since a fat is usually made up of several different fatty acids, mixtures of these fatty acids appear as end products.

Many of the fatty acids appearing as end products of the hydrolysis of fats by *lipase* are just as incapable of passing the protoplasmic membranes of the cells in which they are formed as were the original fats. Consequently, it is likely that the fatty acids are still further broken down to carbohydrates before they can be utilized. Such experimental evidence as is available supports this assumption, but relatively little is known about the mechanism of the process. Glycerol is diffusible and hence can probably be translocated as such, but it is likely that it, too, is changed before it is assimilated.

Digestion of Proteins. While proteins occur in every living cell, they are seldom found in large quantities even in storage regions of plants and hence a study of their digestion within the plant is attended with difficulty. It will be recalled that basically the proteins consist of chains of amino acids. In many of the proteins, other substances are chemically combined

with the amino acids, forming side chains which may exert a considerable effect upon the specificity of proteolytic enzymes. When the naturally occurring proteins are broken down by enzyme action, they may yield, at first, **proteoses** and **peptones**. Both proteoses and peptones are soluble in water and are noncoagulable by heat, but the proteoses can be precipitated by saturating their solutions with ammonium sulfate, while the peptones cannot. Both the proteoses and the peptones are still chains of amino acids but are shorter than those of the original protein. Both are still rather complex compounds. Compounds consisting of two or more amino acids, the carboxyl group of one being united with the amino group of another (peptide linkage), are called **peptides**. Those consisting of two such combined amino acids are called **dipeptides**, and those consisting of many amino acids are called **polypeptides**. The peptides are less complex than the proteoses, peptones, or original proteins.

The hydrolytic enzymes that digest proteins and their derivatives have been classified in several ways. In general, enzymes that attack the original native proteins are called *proteinases*. Examples of these are *papain*, *pepsin*, and *trypsin*. Those which hydrolyze peptides are called *peptidases*. If they hydrolyze dipeptides, they are called *dipeptidases*, and if they hydrolyze polypeptides they are called *polypeptidases*. *Carboxypeptidases* act only on polypeptides containing a free carboxyl group, while *amino-peptidases* act on polypeptides containing a free amino group. The proteolytic enzymes are sometimes separated into two broad groups, the *exopeptidases* and the *endopeptidases*. The *exopeptidases* require a free α -amino or α -carboxyl group adjacent to the sensitive peptide linkage in the main part of the molecule of the substrate and are therefore restricted in their action to terminal peptide bonds. The *endopeptidases* do not require free terminal amino or carboxyl groups and are therefore capable of splitting central peptide bonds of proteins and suitably substituted peptides. Most of the proteinases are endopeptidases, while most of the peptidases are exopeptidases.

The *amidases* are a group of enzymes that usually split off ammonia from *amido* or *amino* compounds. In some cases, urea appears as an end product of their action. *Amidases* are found in many plants, including the fungi as well as higher plants. Among them are *arginase*, which splits the amino acid arginine into ornithine and urea; *asparaginase*, which forms aspartic acid and ammonia from asparagine; *aspartase*, which converts aspartic acid into ammonia and fumaric acid, and *urease*, which hydrolyzes urea to ammonia and carbon dioxide. *Urease* was the first enzyme to be prepared in a pure crystalline form.

The general term *protease* is commonly used for all enzymes that catalyze the hydrolysis of proteins and of protein hydrolytic products such as

proteoses, peptones, and polypeptides. Many *proteases* have been found in plants. Some of the best known are *pepsin*, reported to be present in insectivorous plants, *papain*, obtained from the latex of *Carica papaya*; *ficin*, from the milky sap of several species of fig trees; *bromelin* from ripe pineapples; and *solanain* from the horse nettle (*Solanum eleagnifolium*).

In the plant the end products of protein digestion are the amino acids, with the intermediate production of proteoses, peptones and peptides. The amino acids are carried to growing parts of the plant and are utilized in the resynthesis of proteins and probably other compounds.

Fate of the Products of Digestion. As has been seen in the preceding paragraphs, digestion goes on particularly in regions of the plant where foods are stored. As soon as these foods are digested, they are in a form which enables them to be transported to other parts of the plant, especially to regions where growth is proceeding. Here they are mostly used in building up new protoplasm, new cells, and new tissues; but a large portion of the digested food is also used in these regions to supply the energy needed for growth and for normal physiological function of the plant. In this case, the foods are oxidized or respired. Often foods are digested in one part of the plant, transported to other parts, and converted back again to the original compounds in new storage regions. Thus the starch which accumulates in the leaves of many dicotyledonous plants during the day is digested at night and carried to various storage regions, such as roots, stems, and tubers, and is there reconverted into starch.

In addition, all the various chemical compounds that are synthesized in the plant are made out of the digested foods.

We may summarize the uses made by the plant of the digested foods as follows:

1. They may be carried to other parts of the plant (translocation).
2. They may be oxidized for their contained energy (respiration).
3. They may be converted back to the original compounds in new storage regions (food storage).
4. They may be used in the synthesis of new organic compounds (organic synthesis).
5. They may be used to build new protoplasm (assimilation and growth).

RESPIRATION AND FERMENTATION

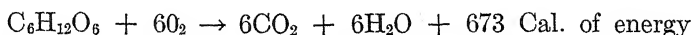
Introduction. As long as an organism is living, it must be supplied with energy to carry on the ordinary life processes. In a previous chapter, reference was made to the fact that plants containing chlorophyll store up radiant energy in the making of carbohydrates by photosynthesis. This stored energy in carbohydrates and other compounds is made available

by the process of **respiration**. Respiration is essentially an oxidation process. In its ordinary form, it implies a chemical reaction in which oxygen combines with some of the constituent elements of the substance being oxidized, thereby forming oxides and liberating energy. Such oxidation occurs, for example, during the burning or combustion of organic substances and results in the liberation of considerable energy in the form of heat. If, for example, we burn sugar, the oxygen of the air combines with the sugar to form carbon dioxide and water, and much heat is liberated. The same thing takes place in the plant but at a much slower rate and at ordinary temperatures. Such oxidation at lower temperatures is made possible by the action of enzymes or, in other words, respiration in the plant is enzymatic in nature. Furthermore, much of the energy liberated does not appear as heat, but is used in carrying on the work of the living cells of the plant. *The term respiration is used in a comprehensive way to include all oxidation, or decomposition, of materials resulting in the liberation of energy, i.e., all catabolic changes involving energy release, and any gaseous exchange accompanying this.* It should be emphasized that the most important feature about respiration is that energy is released by it, and not that oxygen is taken in and carbon dioxide liberated.

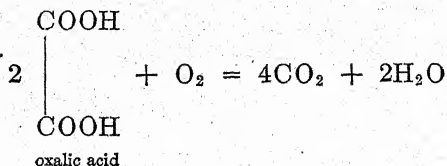
Oxidation may take place in the absence of free oxygen, involving loss of hydrogen or loss of electrons. There are two types of respiration, depending upon whether free oxygen is involved and to what degree the oxidation proceeds, *viz.*, oxygen respiration and anaerobic respiration, or fermentation. **Oxygen respiration** involves the utilization of free oxygen at least in the final stages of the process and results in complete oxidation to carbon dioxide and water. **Anaerobic respiration, or fermentation**, takes place in the absence of free oxygen and results in incomplete oxidation, thus yielding compounds capable of being still further oxidized, such as alcohols and organic acids. It will be shown later that the two types are probably related.

Seat of Respiration in Plants. In the higher animals and man, the lungs, tracheae, and nostrils are often looked upon as organs of respiration, and the inhalation of air and exhalation of carbon dioxide as respiration. In a strict sense, however, this mechanical exchange of gases is not respiration but breathing. In the plant, there are no organs comparable with lungs, but the stomata, lenticels, and intercellular spaces function in gaseous exchange. True respiration takes place in every living cell of plant or animal at all times, day and night. So much is this true that we may look upon a cell as dead if respiration no longer goes on within it. There are, in other words, no special organs of respiration in the plant, but all parts of the plant that consist of living cells carry on the process.

Gaseous Exchange—The Respiratory Quotient. We may represent the complete respiration of glucose by the following equation:



It will be seen from this equation that oxygen is consumed and CO_2 liberated and that the volume of oxygen used is equal to the volume of CO_2 liberated. It is customary to refer to the relation of CO_2/O_2 as the respiratory quotient. Obviously, in the foregoing equation the respiratory quotient would equal 1. In determining the respiratory quotient, it is necessary to measure the oxygen consumed by the plant as well as the CO_2 liberated. When this is done, the values obtained for the respiratory quotient are sometimes less than 1 and sometimes greater. This may be brought about by one or more of the following causes: (1) The carbohydrates may be incompletely oxidized to organic acids or other compounds in which the production of CO_2 does not take place. This would make the quotient less than 1. A typical example of this is found in some of the cacti. In these plants, the respiratory quotient is always less than 1 at night because carbohydrates are oxidized to organic acids. The following day, these organic acids, together with unchanged carbohydrates, are completely oxidized to CO_2 and H_2O and, since less oxygen is required to oxidize the acids, the quotient becomes greater than 1. A similar condition has been found to take place in developing green apples. It might be mentioned that such an arrangement is very useful to the cacti in conserving CO_2 for photosynthesis, since, if complete oxidation occurred at night, much CO_2 would be lost which is actually made available in the daytime. (2) Respiration may take place in the total absence of oxygen, but with the liberation of CO_2 , as in fermentation, making the quotient greater than 1. (3) Other substances besides carbohydrates may be oxidized, yielding different quotients, greater or less than 1. For instance, when fats are oxidized, as frequently happens, the quotient will be less than unity because of a greater amount of oxygen needed to oxidize fats and sometimes because of the fixation of some of the oxygen by unsaturated fatty acids. The respiratory quotient of germinating fatty seeds like sunflower or flax is often as low as 0.3. On the other hand, the oxidation of some of the organic acids yields quotients greater than unity. Thus the complete oxidation of oxalic acid would give a quotient of 4 as seen in the following equation:



In general, the respiratory quotient is equal to unity only when carbohydrates are completely oxidized.

Substances Used in Respiration. From the preceding statements of the fluctuations in the value of the respiratory quotient, it is clear that plants are able to use different substances as a source of energy. Probably the most common material oxidized by the higher plants is either glucose or fructose. Other sugars are also used. Fats, amino acids, other organic acids, and even proteins are oxidized by some plants. In cases of starvation, protoplasm itself may be used in respiration.

Among the bacteria, there exist specialized groups that utilize inorganic materials as a source of energy. Thus the hydrogen bacteria use hydrogen, the sulfur bacteria sulfur, the methane bacteria methane, and the hydrogen sulfide bacteria hydrogen sulfide. These substances are all oxidized as a source of energy.

If the whole plant kingdom is included, we could say that the substances used in respiration range all the way from the simplest inorganic materials to the most complex organic material. In general, however, we may look upon the sugars as the most common respiratory material in the higher green plants.

Energy Relations. It has already been stated that the most important fact about respiration is that it provides energy for the immediate use of the plant. This energy is used by the plant to perform all its physiological functions, but often some of the energy escapes as heat or is transformed to light. In warm-blooded animals, it is respiration that keeps up the body temperature. There is no such constancy of body temperature in plants. As a rule, a plant tends to acquire the temperature of the surrounding atmosphere; but when the respiration rate is very high, it is not unusual for the internal temperature of the plant to exceed that of the surrounding atmosphere. This may occur in germinating seeds and often in opening flowers. Thus the spadix, or flower cluster, within the sheathing spathe of *Arum italicum* has been found to have a temperature of 51°C. when the outside temperature was 15°C. This rise in temperature of flowers resulting from high rate of respiration may contribute to the ability of such plants as skunk cabbage to open flowers as early as February in north temperate regions when the ground may still be frozen. Plants probably never use all the energy produced in respiration for vital purposes. Some of it probably always escapes as heat. A common example of the heat produced by the respiration of germinating seeds is furnished by the rise in temperature of stored grain when it becomes moist.

In certain fungi and bacteria, some of the respiratory energy is transformed into light. This phenomenon is called **bioluminescence**. It is this phenomenon that makes such plants glow at night with a phosphorescent light.

The total amount of energy released in respiration depends upon the kind of material oxidized and upon the completeness of the oxidation. Not all substances yield the same amount of energy. Thus a gram of carbohydrate yields, on complete combustion, 4.1 Cal., a gram of alcohol 7.1 Cal., a gram of fat 9.1 Cal., and a gram of protein 5.8 Cal. If we compare the fats with the carbohydrates, it is obvious that a given amount of fat, on complete oxidation, will yield about $2\frac{1}{4}$ times as much energy as the same amount of carbohydrate. This is because of the fact that fats contain relatively less oxygen. In general, compounds rich in hydrogen or low in oxygen yield more energy than compounds relatively low in hydrogen and high in oxygen. The degree of oxidation is also important in this connection. Thus, if glucose is completely oxidized, as in oxygen respiration, it yields 673 Cal. per gram-molecular weight, while if it is oxidized to ethyl alcohol, as in fermentation, it yields only 24 to 28 Cal. In other words, about twenty-five times as much sugar would be used in fermentation to obtain the same amount of energy as is yielded in complete oxygen respiration.

Factors Affecting the Rate of Respiration—Internal Factors.—The rate at which respiration goes on in the plant is governed by a number of internal as well as external factors. Among the internal factors may be mentioned the amount of respirable material, especially carbohydrate, the amount of cell matter actually respiring, the activity of respiratory enzymes, the acidity of the cell sap, the activity of the plant, and the age of the plant. The internal factors have not all been thoroughly investigated, although some knowledge has been obtained. It has been found, for example, that leaves containing small amounts of sugar, as a result of being kept in the dark, respire very feebly, but when supplied with sugar (in the dark) the rate of respiration immediately goes up. High concentrations of sugars, however, decreased the rate again, probably through osmotic effects, since high concentrations of mineral salts behave similarly. It is natural to assume that the continuance of respiration will depend upon an adequate supply of food and hence the rate of respiration falls when the supply becomes inadequate. In general, young plants respire at a more rapid rate per unit of dry weight than do older plants, partly because a greater percentage of their tissues is active physiologically and hence requires a greater supply of energy. Similarly, dormant organs like seeds and buds respire very feebly, but when growth is renewed the rate of respiration immediately goes up.

Among the most important internal factors affecting respiration are the activities of **respiratory enzymes**. While respiration is oxidation, many of the substances used as a source of energy must first be hydrolyzed before they can be oxidized in respiration. This involves many of the hydrolyzing enzymes already mentioned. Some of the respiratory enzymes catalyze oxidation involving the addition of oxygen, while others catalyze oxidation involving loss of hydrogen or loss of electrons. There are two principal classes of oxidizing enzymes, the *oxidases* and the *dehydrogenases*. These different types of enzymes probably operate together in bringing about oxidation of chemical compounds which are ordinarily considered to be stable. Examples of oxidizing enzymes of the *oxidase* type are the *iron oxidases*, such as the various *peroxidases*, and the *copper oxidases* such as *tyrosinase*, *laccase*, and *ascorbic acid oxidase*. Examples of *dehydrogenases* are *alcohol dehydrogenase*, *glucose dehydrogenase*, and *lactic*

dehydrogenase. *Catalase*, although not an oxidizing enzyme, is usually classified with *oxidases* because its action is closely connected with physiological oxidation. It decomposes hydrogen peroxide into water and gaseous oxygen.

External Factors. Of the external factors that affect the rate of respiration, the most effective are temperature, light, oxygen supply, water supply, carbon dioxide concentration, toxic and stimulating substances, and disease and injury.

Temperature. In general, the rate of respiration increases as the temperature increases, approximately doubling in rate for every 10° rise in temperature. Plants may still continue to respire at very low temperatures, although the rate is very low. This is especially true of dry, dormant structures like seeds. Since some seeds are able to withstand temperatures of -50°C. and lower, and, since respiration continues as long as life continues, some respiration must go on even at such low temperatures, even though it is too feeble to be detected by ordinary means. As the temperature is increased, the rate of respiration increases until a maximum point is reached. Beyond this the rate remains the same until a temperature is reached that kills the plant. While there is some evidence that at higher temperatures the rate of respiration may fall off in some plants, in general it has been found that there is no optimum for respiration. That is, the rate continues to rise with increasing temperature to the maximum rate and stays at that point. In other words, there is no one temperature at which the highest rate of respiration is obtained.

Light. Respiration increases in chlorophyll-containing plants in light, but the effect of light is an indirect one in that it probably operates through supplying respiratory material in the form of carbohydrates. Plants lacking chlorophyll do not respond in this manner. That light is not necessary for respiration is seen from the fact that it proceeds at night as well as in the daytime. It is possible that part of the effect on rate is caused by the rise in temperature resulting from the absorption of radiant energy by the cell constituents. Spoehr explains part of the effect of light by the fact that the sun's rays cause ionization of atmospheric oxygen and this causes autooxidation in the protoplasm. As a result of the effect of light, shade plants often respire at a lower rate than do sun plants.

Oxygen Supply. While it is possible for respiration to continue for a time in higher plants even in the total absence of oxygen, normally a supply of oxygen must be available for the higher plants to continue to live. Whether or not oxygen is present greatly affects the type of respiration and the end products produced. As a rule, there is much more oxygen present in the atmosphere than is needed by plants. Concentrations as low as 1 per cent have been found to be sufficient in some cases. It is probable that many of the interior tissues of plants normally do not obtain very high concentrations of oxygen and hence could not respire normally if large quantities of oxygen were needed. There are some bacteria and fungi that normally live in the total absence of oxygen. Such forms carry on only anaerobic respiration.

Water Supply. The effect of water content on respiration is well known in its effect on seeds. Dry seeds respire at a very slow rate, but as water is absorbed the rate increases up to a maximum which varies with different seeds. A further increase in water may then diminish the rate. It is this increased respiration that causes stored grain sometimes to heat up when it becomes moist. The effect of water in this instance is partly explained by the fact that the water may increase digestive processes which provide respiratory materials. The respiration of the growing plant is also affected by the water content of its tissues. If water is lost by transpiration to such an extent as to render the cells flaccid, growth is checked and with it the respiratory activity.

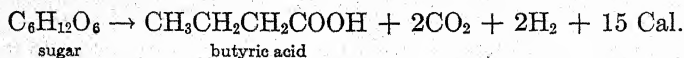
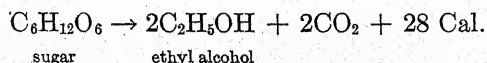
Carbon Dioxide Concentration. The accumulation of carbon dioxide gas resulting from respiration may check further respiration. This is shown by the fact that ger-

mination of seeds is entirely checked if the carbon dioxide is allowed to accumulate around them. When this carbon dioxide is removed, however, germination continues. Green plants in light can stand rather high concentrations of carbon dioxide without injury. The checking effect of carbon dioxide on respiration may partly explain the fact that protoplasmic streaming is stopped by carbon dioxide.

Toxic and Stimulating Substances. The toxic effect of certain chemicals upon plants as well as animals often results from the effect of these substances on respiration. While in strong doses such substances may completely check respiration and thereby cause death, it is interesting to note that many of them in very weak doses speed up the rate of respiration for a while. For example, it has been found that a dose of 0.1 cc. of chloroform in 970 cc. of air causes an increase in the output of carbon dioxide from leaves. After a time, this increase falls back to the normal rate. A dose as great as 1 cc. of chloroform in 970 cc. of air also stimulates carbon dioxide production for a while, but proves to be toxic because there is no recovery of the leaf from it. If the dose is raised to 10 cc. in 970 cc. of air, there is no stimulation at all, and respiration ceases immediately. Ether, acetone, formaldehyde, caffeine, paraldehyde, cocaine, morphine, quinine, solanine, and other substances have been found by various workers to produce similar effects; *i.e.*, a very small dose acts as a stimulant, a large dose as a narcotic. There have been attempts to explain this action of poisons, but none of them is well established. Warburg believes that boundary-surface phenomena play an important role in respiration and that the action of poisons is explained by the fact that they are strongly surface active and hence interfere strongly with respiration. Some toxic materials probably operate through their effects on respiratory enzymes.

Disease and Injury. Disease and injury to the plant often also stimulate respiration. The degree of stimulation depends upon the extent of the injury and the nature of the tissue injured. In some instances, injury induces renewed growth, which results in healing of the wound. This increased growth implies increased respiration in that more energy is being used. In some cases, as in the potato, it has been shown that injury causes an increase in sugars in the injured portion, probably caused by a stimulation of diastase activity. These sugars furnish respiratory material and may contribute to the increased rate of respiration. If the injury or disease is sufficiently widespread in the plant, it may become quite detrimental through the loss of materials resulting from increased respiration, although many other factors contribute to the weakening of the plant.

Anaerobic Respiration—Fermentation. Many plants, when deprived of free oxygen, still continue to give off carbon dioxide and often produce alcohol and other compounds. This has been found to be true of seeds, fleshy fruits, leaves, flowers, woody parts of plants, and many fungi and bacteria. Respiration of this type is called anaerobic respiration, or fermentation. Well-known examples of such fermentations are alcoholic, lactic acid, and butyric acid fermentations of sugar. These may be represented by the following equations:



It will be observed that in each case no free oxygen is involved and that furthermore much less energy is liberated than when the sugar is completely oxidized. All these processes are enzymatic. The first of these processes is made use of in the commercial production of alcohol by yeast. The second occurs naturally when milk sours, and the third causes butter to become rancid. Fermentation processes are widely made use of commercially.

The best known of these processes is alcoholic fermentation brought about by the enzyme complex *zymase*. The fermentation of sugar to alcohol has been practiced by man for centuries. While yeast is commonly employed for this fermentation, many other plants are also capable of carrying it out, particularly other fungi and bacteria as well as higher plants. Pea seeds, after being soaked in water and placed in an inverted test tube of mercury, where they have no access to oxygen, will in a short time produce much carbon dioxide and alcohol. Some plants will die if kept too long under anaerobic conditions. The products of the incomplete respiration which takes place probably contribute to the cause of death since many of them are toxic. Other plants, especially some of the fungi and bacteria, are not injured.

The foregoing equations used as examples of fermentations give merely the initial substrates and the end products of the reactions. It is now known that in each case several intermediate steps take place before the end products are formed. Many different enzymes are involved. The reactions taking place in alcoholic fermentation have been fairly definitely worked out, but they are too complex to be considered in detail here. Briefly, the principal transformations that take place are as follows:

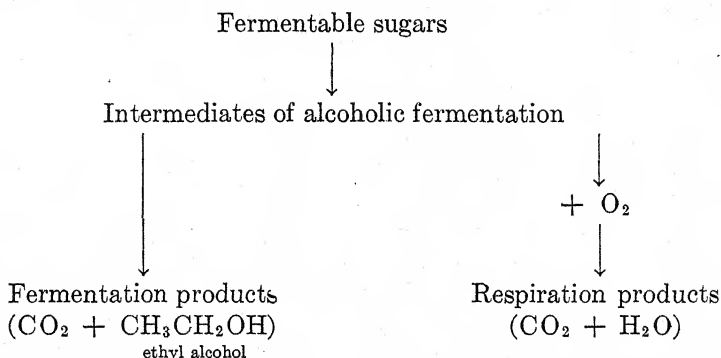
1. In a series of separate reactions involving several enzymes, fermentable sugars combine with inorganic phosphate to form esters of sugar and phosphate, called hexose phosphates, ultimately yielding hexose diphosphate, $C_6H_{10}O_4(H_2PO_4)_2$.
2. The hexose diphosphate, by the action of the enzyme *aldolase*, is split into two 3-carbon phosphoric esters called triose phosphates.
3. The triose phosphates are ultimately converted into pyruvic acid, $CH_3 \cdot CO \cdot COOH$, through the action of several separate enzymes.
4. The enzyme *carboxylase* next splits off CO_2 from the carboxyl group, $COOH$, of the pyruvic acid, thereby converting it into acetaldehyde, CH_3CHO , and CO_2 .
5. Finally, by the action of the enzyme *alcohol dehydrogenase*, the acetaldehyde is converted into ethyl alcohol, CH_3CH_2OH .

The enzyme complex, *zymase*, as found in yeast and other plants, and formerly thought of as a single enzyme, probably consists of all the enzymes mentioned in the foregoing reactions together with other substances.

It should be emphasized regarding fermentation in general that it is a much less efficient method for the plant to obtain energy than is oxygen respiration. Whereas the complete oxidation of glucose, as previously mentioned, yields 673 Cal. of energy per gram-molecular weight, the fermentation of glucose to ethyl alcohol yields only 24 to 28 Cal. It is likely, therefore, that when a growing plant is placed under anaerobic conditions, its death may be partly due to the fact that it is unable to obtain sufficient energy to continue its normal physiological functions. None the less,

there are some plants that make use of this method alone to obtain energy. Some of the bacteria belong to this category. Such plants cannot live in an atmosphere containing free oxygen. The lactic acid bacteria are a well-known group of such plants.

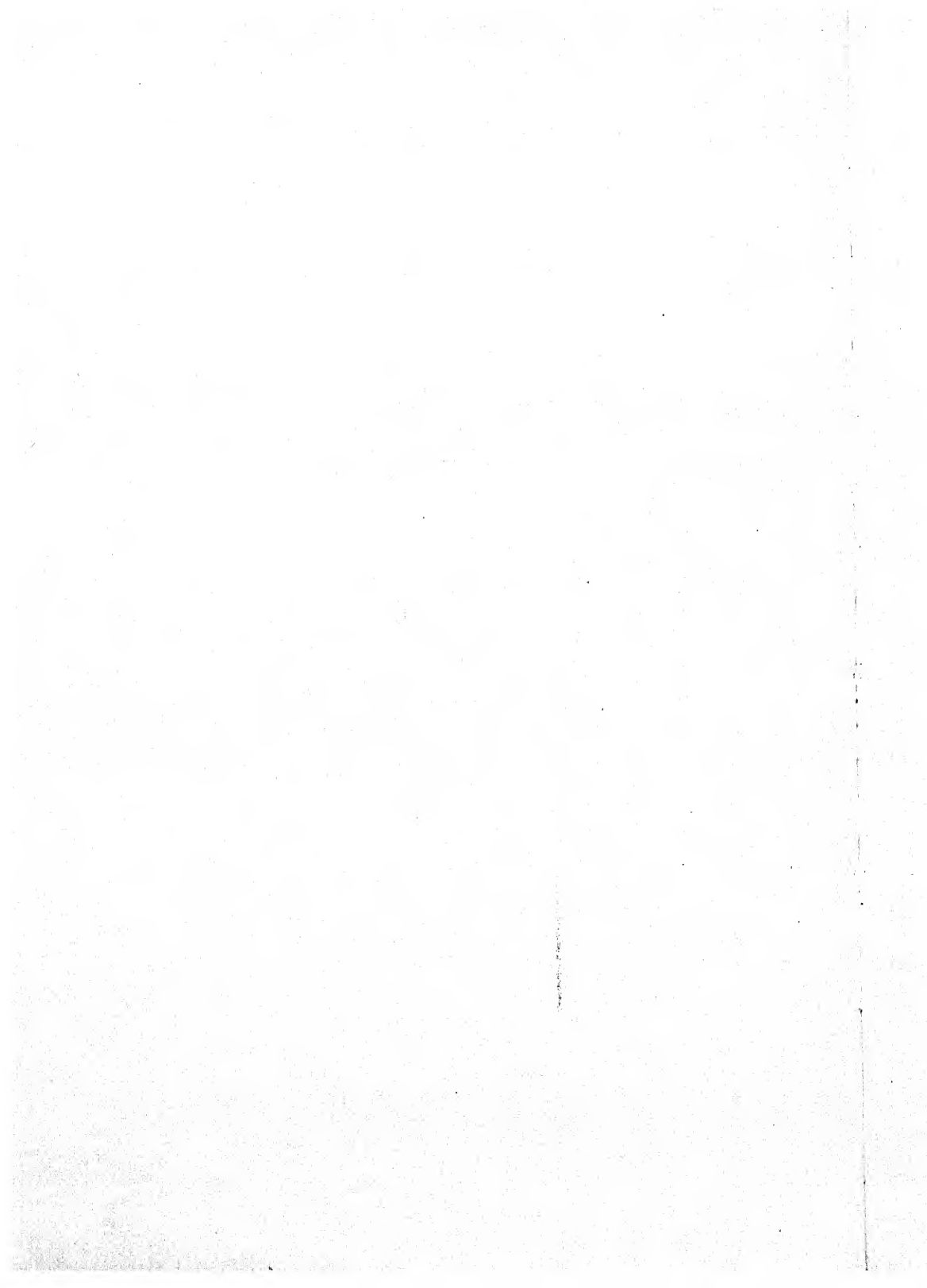
Possible Connection between Oxygen Respiration and Anaerobic Respiration in Higher Plants. It is now generally believed that all respiration in higher plants consists of two phases, an anaerobic phase in which the cleavage of sugar occurs, yielding several intermediate products, and a second phase which takes place with the access of free oxygen and results in the complete oxidation of the intermediate products of the anaerobic phase to carbon dioxide and water. These two phases are commonly represented as follows:



According to this idea, oxygen respiration and anaerobic respiration are alike in the early stages. When the plant has a supply of free oxygen, the intermediate products are oxidized completely to carbon dioxide and water. When the plant is deprived of oxygen, there may be formed alcohol or carboxylic acids and perhaps other substances.

That there is an anaerobic phase of ordinary respiration is supported by the fact that, when plants that require free oxygen are placed in an atmosphere lacking oxygen, they do not die at once but continue to liberate carbon dioxide and usually form alcohol. If such plants are restored to an atmosphere containing oxygen, there is at first an increased production of carbon dioxide, indicating that the unoxidized anaerobic products of respiration are now completely oxidized. It is also obvious that plants requiring free oxygen could not live indefinitely in an atmosphere lacking it, since the accumulated, incompletely oxidized products of the anaerobic respiration would become toxic. Furthermore, the production of these compounds also furnishes an explanation for the development of undesirable flavors and discolorations that occur in stored fruits and vegetables under improper ventilation. This conception also explains why respiration in the plant can proceed at ordinary temperature, since the oxidations involved are brought about by enzymes.

Part II
THE PLANT GROUPS



CHAPTER 13

PLANT CLASSIFICATION AND NOMENCLATURE

The Need of a System of Classification. Probably 350,000 species of plants are known to science and many more remain to be discovered, named, and classified. These plants present great variation as to size, structure, methods of reproduction, mode of life, and ecological and geological distribution over the earth. In order to facilitate the solution of problems dealing with plants, it is therefore convenient to have systems of classification for this large and diverse group of organisms. It is easier to convey to another a clear idea of a kind of tree or a chemical compound by referring to it as a species of oak or as a carbohydrate compound, respectively, than by trying to differentiate it in succession from all other kinds of trees or from all other chemical compounds. The prime reason for a system of classification of living organisms is convenience. It is advantageous, in the interest of brevity and conciseness, to have some way of indicating the relationships of living organisms such as the cone-bearing trees, liliaceous plants, or the rodents among animals.

Kinds of Classification. In general, two distinct types of plant classification may be recognized. A series of plants may be so arranged and classified as to bring out their evident relationships to each other, for it is a fundamental fact of biological science that these relationships are present in varying degrees in all living organisms. A system of classification that attempts to show relationship is known as a **natural system**. Relationships among different groups of living organisms exist because of their descent from a common ancestor. For this reason, related organisms inherit many old, well-established features or traits common to the race as a whole. Divergences recognized in lines or groups come about through the development and evolution of new features or traits, following some change or mutation in their more immediate ancestors. Relationships are determined on the basis of deep-seated similarities which exist within groups, particularly in features which are not easily induced to vary. Among such features are the general form and structure of the body, internal anatomical structures, many features of reproduction, cell structure, and in some cases physiological processes. As an example of natural groups of plants, the gymnosperms and angiosperms may be mentioned. These plants differ in many ways, among which are details of anatomical structure and the manner in which their seeds are borne. The conducting tissue in the wood

of gymnosperms is largely composed of elongated single-celled elements called tracheids, while that of angiosperms characteristically contains long tube-like vessels. These vessels are composed of several cylindrical cells with ends adjoining and constitute the principal water-conducting elements of angiosperms. The gymnosperms, represented in the north temperate climates by the cone-bearing trees such as pine and hemlock, produce their seeds on open scales in the conifers and morphologically homologous structures in other members of the group. In the angiosperms, the structures comparable with the scales of the cone surround and enclose the seeds. Plants usually lacking vessels, but with wood generally composed of tracheids and producing seeds borne on open scales in cones, are recognized as belonging to a natural group, the gymnosperms. Similarly plants containing typical vessels and producing seeds borne enclosed are regarded as belonging to another natural group, the angiosperms. Within the group of gymnosperms, related but also distinct orders and families are recognized as belonging to smaller natural groups. Likewise, within the group of angiosperms, or flowering plants, subgroupings are made on the basis of relationships indicated by such features as the internal structure or arrangement of tissues and the structure of the flower, particularly the stamens and pistils, which again are organs essentially concerned in reproduction. Thus other natural groups such as the lily family and the legume family are recognized.

A second type of classification is one based upon certain minor, more variable, and superficial characters. This is known as an **artificial system** of classification. The old classification of plants into herbs, shrubs, and trees was such a type, but it is now known that many trees are more closely related to certain herbaceous plants than they are to other trees. The classification of flowers on the basis of color, common in popular flower guides, is another example, but the red rose is certainly more closely related to the white rose than it is to a red poppy. Again, plants may be classified on the basis of their relations to water. The ecological groups—hydrophytes (plants that live in or partly in water), mesophytes (plants that live in moist terrestrial locations), and xerophytes (plants that live in extremely dry or desert situations)—represent an artificial classification that tells nothing of natural relationships. In the same way, plants may be artificially classified, on a physiological basis, into parasites and saprophytes, but the parasitic mistletoe and the likewise parasitic germ causing diphtheria are at best only distantly related to each other.

Since either of these types of classification may be more useful than the other under certain conditions and circumstances, both the natural and the artificial systems have persisted side by side. The ecologist finds constant use for an ecological classification, and the physiologist for a

physiological classification. Because they are based upon relationships, natural systems of classification are of greater fundamental importance than artificial ones for an understanding of the plant kingdom.

THE CLASSIFICATION OF THE PLANT KINGDOM

Emphasis upon relationships has led to the development of new groupings of plants in some of the recently proposed classifications. Two systems of classification arranged for comparison are given on pages 328 to 329. The one on the right is an older system that has been in use for many years. The one on the left, prepared by Professor Tippo¹, is a scheme more recently developed that represents an attempt to indicate natural relationships more correctly than was previously possible. These two systems differ in a few important features and several minor details. In the older system, all plants are grouped into four great **divisions** with **classes** listed under each as follows: **division I, Thallophyta**—algae and fungi; **division II, Bryophyta**—mosses and liverworts; **division III, Pteridophyta**—ferns and fern allies; **division IV, Spermatophyta**—gymnosperms and angiosperms. These names are derived from the Greek language and refer to the general characteristics of the plants included in the different groups. The suffix *-phyta* occurring in the name of each of the divisions comes from the Greek and means "plants." The term **Thallophyta** thus means thallus plants, and the division includes plants of low structural organization. Similarly, **Bryophyta** means moss plants, **Pteridophyta**, feathery plants, referring to the feather-like leaves of ferns, and **Spermatophyta**, seed plants.

In the newer systems of classification, two great groups of plants, the subkingdoms, **Thallophyta** and **Embryophyta** are recognized. The subkingdom **Thallophyta** includes the algae, fungi, and other plants low on the scale of evolution. Except for its designation as a subkingdom, it corresponds in general to the older division **Thallophyta**. The subkingdom **Embryophyta** includes all the more advanced groups, *viz.*, the liverworts, mosses, ferns, and all types of seed plants. The name **Embryophyta** refers to plants developing an embryo following the union of gametes during reproduction.

Numerous smaller groupings with names also ending in *-phyta* occur under the subkingdoms. Among these are the **Chlorophyta**, **Rhodophyta**, **Eumycophyta**, and **Tracheophyta**. These names indicate groups of related plants with certain definite characteristics. For example, **Chlorophyta** means green plants and **Eumycophyta** true fungous plants. These groups, here called *phyla* (singular, *phylum*), are more numerous than the older

¹ *Chronica Botanica*, 7(5): 203-206, September, 1942. Published by permission of the author through the courtesy of Dr. Frans Verdoorn, managing editor of *Chronica Botanica*.

ONE OF THE NEW CLASSIFICATIONS PROPOSED FOR THE PLANT KINGDOM

Subkingdom Thallophyta

Phylum Euglenophyta

Euglena, etc.

Phylum Cyanophyta. Blue-green algae

Oscillatoria, etc.

Phylum Chlorophyta. Green algae

Ulothrix, *Oedogonium*, etc.

Phylum Chrysophyta. Yellow-green algae, golden-brown algae, and diatoms

Tribonema, *Dinobryon*, *Navicula*, etc.

Phylum Phaeophyta. Brown algae

Fucus, *Laminaria*, *Ectocarpus*, etc.

Phylum Rhodophyta. Red algae

Nemalion, *Gelidium*, etc.

Phylum Pyrrophyta. Cryptomonads and dinoflagellates

Peridinium, etc.

Phylum Schizomycophyta. Bacteria

Bacillus, etc.

Phylum Myxomycophyta. Slime moulds

Fuligo, *Stemonitis*, etc.

Phylum Eumycophyta. True fungi

Class Phycomycetes. Algal fungi

Class Ascomycetes. Sac fungi

Class Basidiomycetes. Club fungi

(Fungi Imperfecti). Imperfect fungi

Subkingdom Embryophyta

Phylum Bryophyta (Atracheata). Mosses and liverworts

Class Hepaticae. Liverworts

Class Musci. Mosses

Phylum Tracheophyta (Tracheata)

Subphylum Psilopsida

Class Psilophytinae

Order Psilophytales

Rhynia, *Asteroxylon*, *Psilophyton*, etc.

Order Psilotales

Psilotum and *Tmesipteris*

Subphylum Lycopsidea

Class Lycopodiinae

Order Lycopodiales. Club mosses

Lycopodium and *Phylloglossum*

Order Selaginellales. Small club mosses

Selaginella

Order Lepidodendrales. Giant club mosses

Lepidodendron, etc.

Order Pleuromeiales

Pleuromeia

Order Isoetales. Quillworts

Isoetes

Subphylum Sphenopsida

Class Equisetinae

Order Hyeniales

Hyenia

Order Sphenophyllales

Sphenophyllum, etc.

Order Equisetales. Horsetails

Equisetum, *Calamites*, etc.

Subphylum Pteropsida

Class Filicinae. Ferns

Order Coenopteridales

Botryopteris, etc.

Order Ophioglossales. Adder's-tongue ferns

Ophioglossum, *Botrychium*, etc.

Order Marattiales. Marattiaceous ferns

Marattia

Order Filicales. "True" ferns

Polypodium, *Pteris*, *Azolla*, etc.

Class Gymnospermae

Subclass Cycadophytæ

Order Cycadofilicales (Pteridospermae). "Seed ferns"

Lyginodendron, etc.

Order Bennettitales

Bennettites, *Williamsonia*, etc.

Order Cycadales

Zamia, *Cycas*, etc.

Subclass Coniferophytæ

Order Cordaitales

Cordaites, etc.

Order Ginkgoales

Ginkgo

Order Coniferales

Pinus, *Taxus*, etc.

Order Gnetales

Gnetum, *Ephedra*, and *Welwitschia*

Class Angiospermae

Subclass Dicotyledoneae

Order Ericales (Ranales) "Archichlamydeae", etc. ("Choripetalae")

Order Ericales "Metachlamydeae", etc. ("Sympetalae")

Subclass Monocotyledoneae

THE OLDER CLASSIFICATION OF THE PLANT KINGDOM

Division Thallophyta

Subdivision Algae

Class Euglenineae

Euglena

Class Cyanophyceae. Blue-green algae

Gleocapsa, *Oscillatoria*, *Rivularia*, etc.

Class Chlorophyceae. Green algae

With several orders and genera as *Volvox*, *Ulothrix*, *Oedogonium*, *Spirogyra*, etc.

Class Chrysophyceae. Yellow-green algae

Class Bacillariophyceae. Diatoms

Class Phaeophyceae. Brown algae

Ectocarpus, *Laminaria*, *Fucus*, etc.

Class Rhodophyceae. Red algae

Nemalion, *Batrachospermum*, *Polysiphonia*, etc.

Subdivision Fungi

Class Schizomycetes. Bacteria

Class Myxomycetes. Slime molds

Class Phycomycetes. Alga-like fungi

Saprolegnia, *Rhizopus*, etc.

Class Ascomycetes. Sac fungi

Peziza, powdery mildews, etc.

Class Basidiomycetes. Club fungi, rust fungi, mushrooms, coral fungi, etc.

Class Fungi Imperfecti. Imperfect fungi

Division Bryophyta

Class Hepaticae. Liverworts

Marchantia, *Riccia*, *Pellia*, etc.

Class Musci. Mosses

Sphagnum, *Mnium*, *Polytrichum*, etc.

Division Pteridophyta

Class Psilophytinae

Order Psilophytales

Several fossil genera

Order Psilotales

Psilotum and *Tmesipteris*

Class Lycopodiinae

Order Lycopodiales. Club mosses

Lycopodium and *Phylloglossum*

Order Selaginiales. Little club mosses

Selaginella

Order Lepidodendrales. Giant club mosses

Fossil forms, *Lepidodendron*, *Sigillaria*, etc.

Order Isoetales. Quillworts

Isoetes

Class Equisetinae

Order Equisetales. Horsetails

Equisetum

Order Sphenophyllales

Fossil forms, *Sphenophyllum*, etc.

Order Calamitales

Fossil forms, *Calamites*, etc.

Class Filicinae

Order Ophioglossales. Adder's-tongue ferns, and grape ferns

Ophioglossum, *Botrychium*, etc.

Order Marattiales. Marattiaceous ferns

Marattia, *Danaea*, etc.

Order Filicales. True ferns

Polypodium, *Pteris*, *Marsilea*, etc.

Division Spermatophyta

Class Gymnospermae

Order Cycadofilicales. Pteridosperms or seed ferns

Fossil forms, *Lyginodendron*, etc.

Order Bennettitales

Fossil forms, *Williamsonia*, etc.

Order Cycadales. Cycads

Zamia, *Cycas*, *Dioon*, etc.

Order Cordaitales

Fossil forms, *Cordaites*, etc.

Order Ginkgoales

Fossil forms and the living genus, *Ginkgo*

Order Coniferales. Conifers

Pinus, *Tsuga*, *Taxus*, etc.

Order Gnetales

Gnetum, *Ephedra*, *Welwitschia*

Class Angiospermae. Flowering plants

Subclass Dicotyledoneae. Dicots

Orders Ranales, Magnoliales, Rosales, etc.

Subclass Monocotyledoneae. Monocots

Orders Graminales, Liliales, Orchidales, etc.

groups designated as divisions. Besides the difference in terminology, the groups designated as phyla are not only smaller and more numerous than the older divisions but they correspondingly include less diverse groups of plants than the larger divisions of the older system. The term *phylum* has certain advantages over *division* as the designation of a natural group. The term, meaning line, emphasizes relationship among the organisms in the designated group. Besides this, *phylum* is used in the classification of animals by zoologists. Its use in plant classification thus helps to bring the two systems into better accord. The most serious objection to the use of the term phylum in plant classification is the fact that it is not recognized by the International Botanical Congress, which considers division the proper designation of the great groups of the plant kingdom. Thus, the term division has the official sanction of the International Botanical Congress and phylum does not.

Another conspicuous departure from the older scheme is recognition of the **Tracheophyta** as a phylum, or division, of the plant kingdom. It includes all vascular plants in one group and thereby eliminates the older and diverse groups, the divisions **Pteridophyta** and **Spermatophyta**. In the **Tracheophyta** similarity in the possession of a vascular system is emphasized. As a corollary, the diversities existing among the lower vascular plants, such as lycopods, ferns, and horsetails, are emphasized in a manner to bring out their divergence. By placing the ferns and seed plants in the same subdivision, the **Pteropsida**, obvious similarities between these groups are brought out.

In both the old and the new systems of classification, the larger groups called divisions and phyla, respectively, have been further separated into subdivisions or subphyla. These in turn are separated into classes, the classes into orders, the orders into families. These groups have been further subdivided in great detail, the families into genera, the genera into species, and sometimes the species into varieties. Thus, in the **division** (or **phylum**) **Tracheophyta**, there are subdivisions (or subphyla) the **Psilopsida**, the **Lycopsida**, the **Sphenopsida**, and the **Pteropsida**. Under the **Pteropsida** are found several classes and numerous orders. One of these classes is the Filicinae with the order Filicales, or the true ferns, the family Polypodiaceae with *Polypodium*, *Pteris*, and other well-known genera. Again there is the class Angiospermae with the subclass Monocotyledonae and one of its orders the Liliales, the family Liliaceae with the genus *Lilium*.

The following adaptation¹ of the foregoing systems of classification is used in the discussions that follow.

¹ The authors wish to acknowledge their indebtedness for suggestions to Professor Loren C. Petry of Cornell University, where a similar classification is in use.

features among which are: two cotyledons in the embryo; flower parts mostly in fours and fives; leaves with netted veins; starch generally the photosynthetic storage product; many orders, families, and genera.

Order Ranales. Genus *Ranunculus*, or buttercup.

Order Rosales. The roses. Genus *Rosa*, the rose.

Order Geraniales. Genus *Geranium*, the common geranium, etc.

NOMENCLATURE

The groups of plants, both large and small, are designated by names for accuracy and brevity of reference. Possibly, some numerical or symbolic system might have been worked out, but biologists have used names to indicate the groups of plants and animals.

Common versus Scientific Names. Two methods of naming plants have always been in vogue, the one more for the convenience of the amateur botanist or the layman, and the other for the more technically trained student. Consequently, there has grown up a system of common names for plants and likewise a system of scientific names. Names from either of these systems may be bodily transplanted into the other system and be widely used. Thus the names aster, citrus, catalpa, chrysanthemum, rhododendron, and many others are used interchangeably as common and scientific names. Neither common nor scientific names are always so simple as are these examples. Common names may consist of a noun and any number of qualifying adjectives, as the "purple-flowered milkweed" and the "small, southern, yellow orchid." A complete scientific name consists of only two parts. Their derivation and significance are discussed in the following paragraphs.

At this point it may be noted that, while a scientific name is absolutely specific in application, referring to one definite kind of plant and one only, and moreover is world-wide in application, the same is not true of the common names. Thus it is evident that there may be more than one species of white rose, and the white rose of one locality may not be the same as the white rose of another. The definiteness of scientific names is one of their great advantages over common names.

The Binomial System. The desirability of having all plant names constructed on the same plan will be readily appreciated. This idea, however, was not generally accepted until about the middle of the eighteenth century. Prior to that time, as previously stated, the plants known to botanists were few in number and there was little system in designating them. Usually it was sufficient to refer to each plant with a short descriptive phrase, as a farmer with half a dozen cows might refer to each animal by some such descriptive phrase as "the long-horned red cow." But when his herd of cows increased to a larger number, he might have more than one long-horned red cow and he would be more inclined to designate each cow with a short individual name, not necessarily descriptive in character.

Thus we find the earlier botanists designating a species of mint with the following Latin phrase: *Prunella magna flore albo* (prunella with the large white flower); a species of nasturtium, *Nasturtium hortense latifolium Hispanicum* (the Spanish broad-leaved garden nasturtium); *Asparagus sylvestris foliis acutis* (wild asparagus with sharp leaves). Such a method was cumbersome, to say the least, and as additional new kinds of plants were recognized the inadequacy of the method was apparent.

In 1753, there appeared a monumental work entitled *Species Plantarum* by the great Swedish naturalist Linnaeus (Karl von Linné), in which there was perfected the scheme of the present **binomial system** of nomenclature. The idea underlying this scheme is to designate every kind of plant with a binomial, *i.e.*, a name consisting of two parts. The first part of the binomial is the **genus** or **generic name**, and the second part is the **species** or **specific name**. Moreover the name of the botanist (or an abbreviation) first using this designation is often written following the binomial. Thus the abbreviation "Linn." in the name *Rosa alba* Linn. signifies that the botanist Linnaeus originally gave the name *Rosa alba* to this particular kind of rose. The rules regulating botanical nomenclature provide that once a binomial has been applied to a plant, the same name can never legitimately be used to apply to any other species of plant. That is, there can be but one *Rosa alba*, and the plant to which Linnaeus gave that name in 1753 is still so known today and will continue to be so designated in the future. This method of naming plants put the science of nomenclature on a firm foundation and is the basis of the present system.

The reader will already have noted that scientific names are not derived from the English language but come mostly from either the Latin or the Greek. The early botanists realized the advantages of uniformity in the origin of scientific names and practiced the plan of formulating plant names from the most widely known language in use by scholars of the time, which, in the earliest times, was the Greek but later, and more nearly coincident with the development of botany, was Latin. Even at the present time, Latin is almost universally used in naming new species of plants.

Minor variations often occur within a given species of plant. Such variations may be too slight to justify the application of a new specific name, yet are of sufficient importance to be designated. This is particularly true of cultivated plants. In this instance a new name, called the **variety name**, is added to the binomial, and the name becomes in fact a **trinomial**. Thus *Pyrus malus albiflorus* designates a white-flowered variety of the common apple. In the same way, the "Smith Cider," the "Baldwin," or the "Northern Spy" apples are varieties of a common species known under the binomial *Pyrus malus*.

How Names Are Chosen. The names that are chosen (either scientific or common) are usually significant when their meaning is known. They are usually chosen to represent one of the following situations:

(1) The name may refer to one of the chief characteristics of the plant, as intimated in the "white rose," the scientific name of which is *Rosa alba*, the "lobed spiraea" (*Spiraea lobata*), the "showy orchid" (*Orchis spectabilis*), or the "large rhododendron" (*Rhododendron maximum*). (2) It may be chosen from the character of the habitat, *i.e.*, the kind of substratum on which the plant grows. For example, there is the "water buttercup" (*Ranunculus aquaticus*). (3) It may be chosen to represent the geographical range or a part of it, as in the "New England aster" (*Aster novae-angliae*) or the "Missouri aster" (*Aster missouriensis*). (4) It may be taken from the name of the discoverer of the plant, as "Drummond's aster" (*Aster Drummondii*), or "Harper's Carex" (*Carex Harperi*). Other origins are sometimes met with, but these are the common ones.

Group Names in the Binomial System. The varietal name, the specific name, and the generic name have already been considered. A **variety** may be defined as a type of plant departing in certain very minor respects from the species to which it belongs. The **species** is the common unit of plant classification, designating those plants that are so similar that they might have had a common parentage. No other test for the validity of a species is possible. Species are grouped into **genera** (plural of **genus**). A **genus** may be defined as an assortment of closely related species evidently more closely related among themselves than to the individuals of any other group.

Groups of related genera are in turn combined into larger units termed **families**, which are frequently named for a prominent genus of the group with the addition of certain Latin endings. Thus family names regularly end in *-aceae*. Families are further grouped into orders, which end in *-ales*. For example, the order Liliales includes the family Liliaceae and several other related families. Orders are combined into **classes** ending in either *-ae* or *-eae*, classes into **subdivisions**, and subdivisions into **divisions**, the names of which end in the Greek word *-phyta*. Finally the divisions make up the plant kingdom. The names of **species** and **genera** have diverse endings among which *-a*, *-ea*, *-ia*, *-i*, *-is*, *-um*, and *-us* are common. The following outline of the position of the "Golden Delicious" apple illustrates this usage.

Division Tracheophyta

Subdivision Pteropsida

Class Angiospermae

Subclass Dicotyledonae

Order Rosales

Family Rosaceae

Genus *Pyrus*

Species *malus*

Variety Golden Delicious

Pyrus malus is the scientific name, or binomial, of the cultivated apple. The names of the other groups are not used unless it is desired to indicate the position of this species in the general scheme of classification.

The Number of Plant Species. On page 325 the number of known species of plants is estimated at 350,000. According to G. Neville Jones there may be as many as 107,000 species of Thallophytes, 23,000 species of Bryophytes, and 10,000 species in the group earlier designated as Pteridophytes.¹ He states that estimates of all Angiosperms, or flowering plants, vary from 133,000 to 175,000. Differences in the estimates occur because there are divergent opinions as to the authenticity of many of the named species. Some botanists recognize a greater number of plant groups as true species than others do.

¹ *Science* 94: 234, September, 1941.

CHAPTER 14

THALLOPHYTA—ALGAE

INTRODUCTION

The **Thallophyta**, or thallophytes, constitute a large group of the plant kingdom which includes the oldest and most primitive types of plant life. These plants vary in size from microscopic forms to large brown seaweeds which, in length of main axes, equal or surpass the heights of the tallest trees, although in mass and dry weights they are only a fraction of these large land plants.

Two great groups of thallophytes variously designated as divisions, subdivisions, phyla or classes, depending upon the system of classification, are recognized, the **algae** and the **fungi**. Algae are characterized by the general presence of chlorophyll and fungi by its absence. The two groups can be contrasted in few other general features. Some fungi resemble certain algae sufficiently to suggest close relationships and possibly common origins. Typically algae grow in water or on damp soil and sometimes as endophytes in the tissues of other plants and of animals. Fungi grow in even more diversified habitats. Some of them are aquatic and some terrestrial, growing on decaying organic matter in the soil or on debris. Other kinds of fungi grow as parasites in the tissues of plants and animals where they cause diseases. Collectively algae, fungi, and bacteria make up most of the soil flora regarded as important in soil fertility.

The members of the thallophytes, both algae and fungi, are plants of simple structure and organization. The most primitive consist of a single cell. Others are simply aggregations of cells essentially all alike or usually showing only a small amount of differentiation. Certain species of the large brown algae, however, show diversified organization of plant body. They have strong holdfasts, attaching them to rocks, long flexuous stem-like structures, and an expanded blade portion. Some of these plants have considerable differentiation of tissues that is strongly suggestive of the elaborate tissues in the higher plants. In general, thallophytes are without the well-developed tissue systems characteristic of the higher plants, especially the xylem and phloem of the vascular system. Because of the relatively simple tissue structures and the absence of a well-developed vascular system the plant body is regarded as a thallus, as indicated in the name **Thallophyta**.

Thallophytes have numerous methods of reproduction both sexual and nonsexual, or asexual. An important feature of the thallophytes is that the sex organs are mostly unicellular structures and are not surrounded by covering tissues. This is in contrast with the multicellular sex organs of the higher groups, as typified by the archegonium of the bryophytes.

Classification of the Thallophyta, with classes and orders, may be noted on pages 331 to 332.

THE MYXOPHYCEAE—BLUE-GREEN ALGAE

Introduction. The Myxophyceae (sometimes called Cyanophyceae), or blue-green algae, constitute a small class of primitive plants not closely related to the main group of the algae. They inhabit damp terrestrial places or are entirely aquatic, reaching their best development in stagnant waters abounding in decaying organic materials. Either they are strictly unicellular plants or the cells are joined in a loose organization that may be termed a colony. These colonies are of various forms including irregular, spherical, square, and filamentous types (Fig. 131). In most of them there is no cell differentiation, each cell behaving as a complete unit in itself, but in others there is a distinct cell differentiation that makes it difficult to consider the plant body other than a multicellular plant. Other characteristics of the Myxophyceae are (1) a primitive and simple cell structure, (2) a general blue-green coloration of the plant body, and (3) simple reproductive methods that are entirely asexual in character. A consideration of these points in detail forms the fundamental basis of this study.

Structural Development and Form. The plant body in the Myxophyceae is either a single cell or a group of cells forming a colony. The single isolated cell is, of course, the simplest condition, though by cell division these individuals finally become aggregated into loose masses not definite enough in form to be regarded as colonies. Each cell consists of a single protoplast surrounded by a gelatinous sheath (Fig. 131, *D-F*). From such isolated individuals or indefinite colonies, we may regard the development of colony formation as proceeding along three lines: (1) an aggregation of cells culminating in a rather definitely spherical colony of either a few or a large number of cells as in *Gloeocapsa* and other forms; (2) an aggregation of cells all in one plane, forming a flat square colony of a single layer of cells as in *Merismopedia*; (3) a single line of cells placed end to end, forming a long chain or filament, as in *Nostoc* and other genera (Fig. 131).

The three types of colonies mentioned above have been developed in other groups of plants besides the blue-green algae and form an interesting case of what is known as parallel development, *i.e.*, the production of essentially the same type of organ or plant body by two or more groups of plants that are quite unrelated. In the bacteria and

in the lowest order of the green algae, all the colonial types of the Myxophyceae are duplicated except the filamentous form, which is, however, the form of hundreds of species of the higher orders of green algae. The matter of duplication in form and function, or parallelism, furnishes the topic of discussion in another section of this volume.

The development of these types of colonies in relation to cell division may be thought of as caused by the progressive restriction of the planes

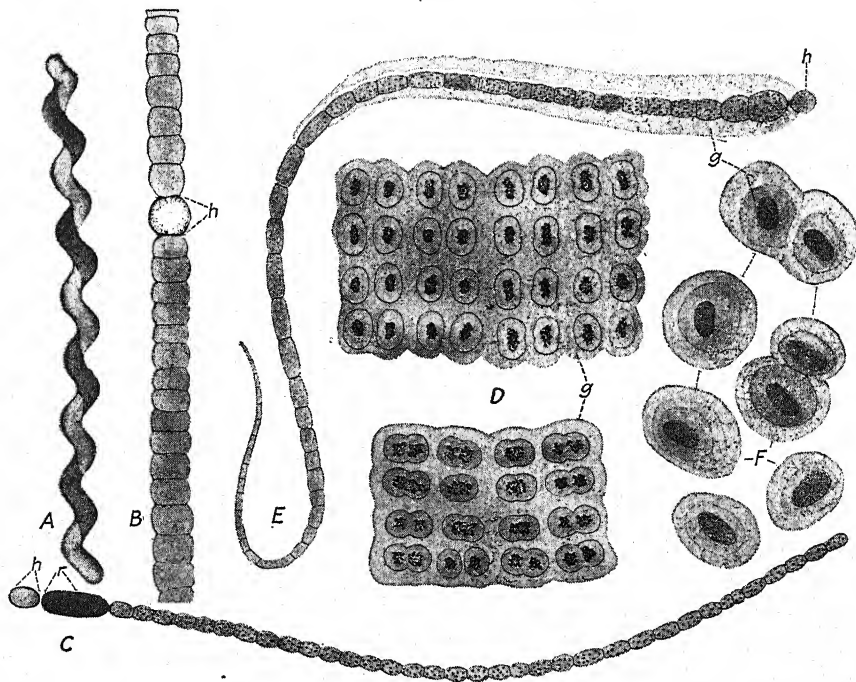
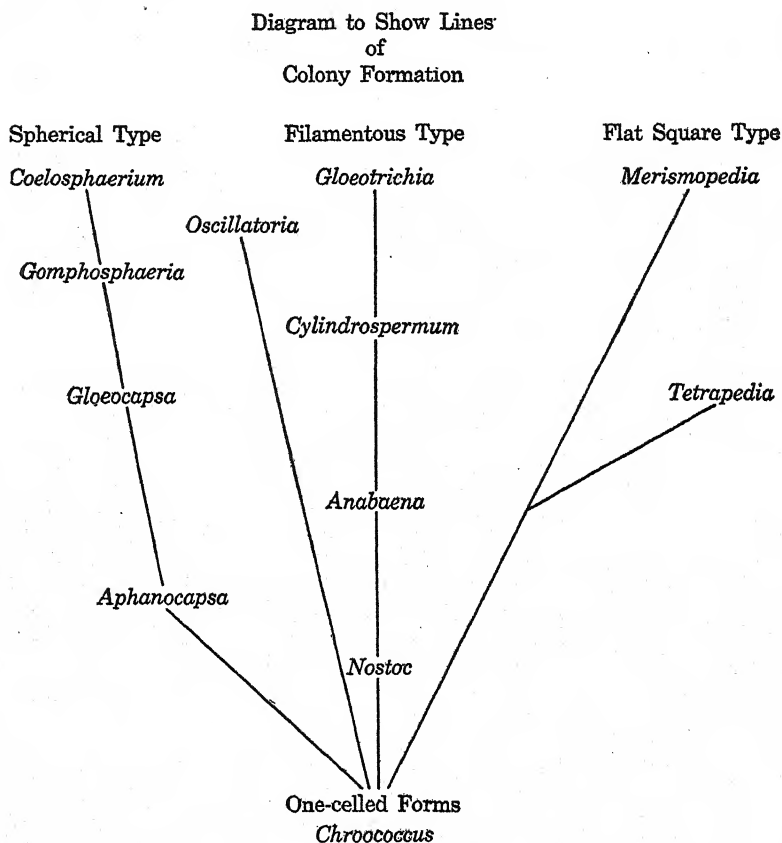


FIG. 131. Blue-green algae. A, *Spirulina*, vegetative form; B, *Anabaena*, vegetative filament with heterocyst, h; C, *Cylandrospermum*, filament mainly composed of vegetative cells, but with basal heterocyst, h, and resting cell, r; D, *Merismopedia*, with cells in early stages of division at right and later stages at left, all imbedded in a gelatinous matrix, g; E, entire filament of *Gloeotrichia*, showing gelatinous sheath, g, and basal heterocyst, h; F, cells of *Gloeotheca*, each central protoplast surrounded by one or more gelatinous sheaths, g.

and directions in which cell division may take place. In the production of spherical colonies the cells divide in all directions, and the colonies increase equally in length, breadth, and thickness. *Gloeocapsa* represents the beginning of this type of development. In some genera the colony attains a definite spherical shape of considerable size. In some cases a colony is formed consisting of a single layer of cells on the periphery, the interior of the sphere being hollow. To attain this, the direction of cell division must be restricted to the curved surface of the sphere.

The flat square type of colony is best illustrated by *Merismopedia*,

a colony of from 16 to several hundred cells, always in multiples of 4 and all arranged in a single plane. To obtain such a colony, cell division must be restricted to two directions in a single plane, resulting in increase in length and breadth but not in thickness (Fig. 131, D).



The filamentous colony is formed when cell division occurs in a single direction, in a single plane, resulting in a chain of cells that, with each cell division, increases in length only. Differentiation of cells in the colony has proceeded further in some of the filamentous colonies than in any of the other types. In fact, in all the other types, the cells remain practically undifferentiated, while in the filamentous forms the question may well be raised as to the propriety of calling the entire filament a multicellular plant rather than an aggregation of one-celled plants. For example, in *Gloeotrichia* (Fig. 131, E) and in *Rivularia*, the heterocyst, a specialized cell described later, always occupies a basal position, resting cells are always located next to it, while the vegetative cells gradually taper in size to a whip-like extremity at the other end. However, the best authorities

regard all such multicellular aggregations as colonies of so many plants rather than as individual plants of multicellular construction.

The Cell Structure. The investigation of the cell structure of the blue-green algae has been an interesting, though difficult, problem. The interest centers around the fact that these plants are universally recognized as constituting a primitive group, and the investigation of the cell structure should, therefore, shed some light on the question of the origin and development of the highly organized protoplast of the higher plants. These

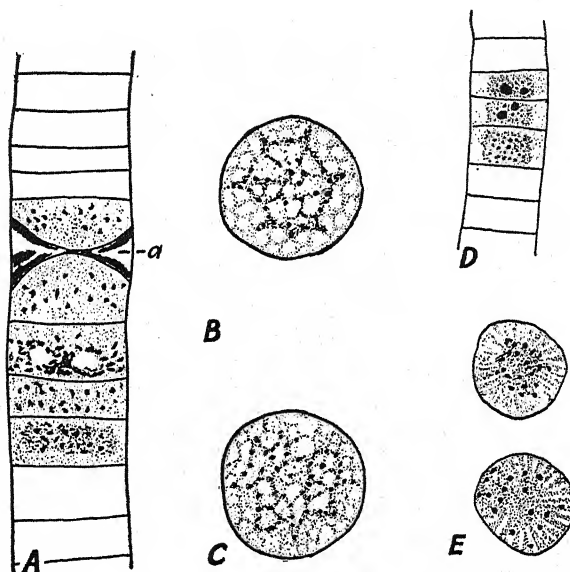


FIG. 132. *Oscillatoria*. A, cells of a filament showing granular contents; also a dead or concave cell at *a*; B, C, and E, cross-sectional views, showing central body and peripheral cytoplasm; D, cells of a filament, showing central body.

investigations have often led to contradictory results or to conflicting interpretations; consequently, the problems that have been considered are by no means all solved. The statement that the cell organization within the group of blue-green algae is of a very primitive type is in full accord with the current opinion on the subject, and this idea may constitute one of the fundamental principles in the study of the Myxophyceae.

The main questions presenting themselves for answer are those concerning the nature and structure of the nucleus, the cytoplasm, and the chloroplast. The protoplast shows two vaguely defined regions, a clear structure, the so-called "central body," and a peripheral portion surrounding the central body (Fig. 132). The coloring matter of the cell is located in this outer portion of the protoplast. These parts have been variously interpreted. Some investigators have regarded the central

body as the cytoplasm and the outer portion as the chloroplast, considering the cell to lack a nucleus. Others have regarded the central body as the nucleus and the outer portion as the cytoplasm, the cell lacking chloroplasts but containing chlorophyll in minute granules. From recent investigations it seems best to regard the central body as a primitive or incipient nucleus, illustrating a step by which the nuclei of the higher plants may have developed. The peripheral or outer portion of the protoplast is then considered to be cytoplasm or a structure corresponding to the cytoplasm of the cells of the higher plants.

The Central Body or Primitive Nucleus. The outstanding fact about the central body or incipient nucleus of the blue-green algae is that it has no limiting membrane, a structure characteristic of nuclei of the higher plant cells. The central body, often radiate in form, is of irregular shape, depending upon the shape of the cell, and occupies about one-fourth to one-third the total volume of the cell. The body appears to have a network of a colorless material, in the meshes of which are embedded granules of chromatin. It is interesting to note that the network of the central body is continuous with a similar network in the cytoplasm. There are other granular substances in the central body besides those of chromatin, but the latter constitute the important content of that body. West, the great English authority on the algae, states that the central body should be regarded as a primitive or incipient nucleus.

The Cytoplasm, Pigments, and Inclusions. The cytoplasm surrounds the incipient nucleus and contains the pigments of the cell, together with various kinds of food reserves in granular form, and other inclusions. The pigments commonly present are chlorophyll, carotene, xanthophyll, and phycocyanin. The first three of these pigments are the ones found in all green plants and have already been described in Chap. 2. Phycocyanin is a blue water-soluble pigment held in solution in the water of the cytoplasm. Together, these pigments are responsible for the characteristic blue-green color of the Myxophyceae. The chlorophyll, carotene, and xanthophyll are considered to be in minute granules suspended in the cytoplasm. Some authors have considered these granules as possibly representing primitive chloroplasts. Besides the pigments mentioned, a red pigment is found in some marine forms, which sometimes obscures the other pigments and gives the water in which such forms occur a bright-red color, as in the Red Sea.

The Cell Wall and the Gelatinous Cell Sheath. Each protoplast is surrounded by a cellulose cell wall and this in turn by a gelatinous sheath. The gelatinous, or mucilaginous, cell sheath is composed of layers and is often colored. The presence of this sheath is an advantage to the plant when exposed to dry conditions, as the gelatinous materials conserve the moisture and preserve the living cell contents from desiccation.

Cell Differentiation. Some, though not extensive, differentiation of the cells is found in the colonial forms of the blue-green algae. In some of the filamentous forms, as in the genera *Nostoc*, *Cylindrospermum*, and *Anabaena*, certain cells called **heterocysts** occur at irregular intervals in the filament (Fig. 131, *B*). These heterocysts are somewhat larger than the ordinary vegetative cells of the filament and are filled with a homogeneous material. In the early stages of their development, pores connect the heterocysts with the vegetative cells, but later the pores are closed by the gradual thickening of the walls of the heterocyst. The function of the heterocyst is in doubt, and in fact it is not certain that it has any definite function besides serving to separate the threads into sections called **hormogonia** (singular, hormogonium). It has been suggested that the heterocysts serve as receptacles of stored food materials. Another theory advanced suggests that they are the remnants of reproductive organs which, for some reason or other, have degenerated as the processes of evolution have progressed. In the genus *Oscillatoria* there are no true heterocysts, but the hormogonia are delimited by dead cells known as **concave cells** (Fig. 132, *A*). Further differentiation of cells occurs in the reproductive processes of some species when heavy-walled **resting cells** (erroneously called spores) are formed (Fig. 131, *C*).

Nutrition. Since these plants contain chlorophyll, they are capable of manufacturing their own carbohydrate foods from carbon dioxide and water through the agency of sunlight. This process has already been studied in seed plants under the name of photosynthesis. The aquatic blue-green algae obtain the water and carbon dioxide by osmosis and diffusion, respectively, from the medium in which they are growing, the carbon dioxide being in solution in the water. Terrestrial species of the Myxophyceae obtain their water from the damp substratum on which they grow, but probably at least a portion of their carbon dioxide is derived from the air. The product of photosynthesis in these plants is a sugar which is later changed into glycogen for storage. In this respect they differ from higher plants in which starch is the usual form in which carbohydrates are stored. Nitrogenous materials are present in the cells in various forms, such as nucleoproteins and albumins. Oil droplets are often present, indicating the synthesis of fats by the protoplast. In general, therefore, these plants have nutritive processes that are very similar to those in higher plants. Certain forms of the Myxophyceae are thought to be able to fix atmospheric nitrogen.

Reproduction. The methods of multiplication and of reproduction are entirely asexual and entirely by means of nonmotile structures. The lack of motile structures in organisms living in water is an unusual condition. All methods are extremely simple.

Cell Division. In all unicellular plants, cell division is the chief method

by which increase in number takes place. In multicellular plants, cell division ceases to be a method of reproduction and becomes instead a method of growth. In the blue-green algae the exact mechanism of cell division is in dispute, some investigators claiming for the forms they have investigated only a simple form of amitosis, while others, working with different species, report in some cases a simple type of spindle formation and other evidences of a primitive mitosis. It is not unlikely that both of these conditions actually exist.

Fragmentation. As an aid to dissemination of these plants, fragmentation of the colony plays an important part, though it is doubtful if it can be regarded as a method of reproduction. When a colony reaches some size, it breaks up, usually as a result of mechanical influences, and each part is the beginning of a new colony which increases in size until the same process is repeated. In the filamentous species, the filaments usually break at the heterocysts. The hormogonia are thus set free, and each of them will again become a mature colony. It may be noted that, if these filaments are regarded as multicellular plants, fragmentation becomes a true method of reproduction.

Resting Cells. Resting cells (sometimes erroneously called spores) may be developed under certain conditions in several genera of these algae (Fig. 131, C). These are heavy-walled cells capable of resisting long periods of unfavorable growing conditions. They are formed from the ordinary vegetative cells, which increase in size and become thick walled and resistant. It is to be noted that the formation of these cells is merely a method of enduring unfavorable conditions and is doubtfully classed as a reproductive process. These cells contain little water and their content has a highly granular appearance.

Summary of the Characteristics of the Blue-green Algae. The outstanding characteristics of the blue-green algae, one of the most primitive groups of the thallophytes and the lowest of the present-day algae, are (1) the simple cell structure with its primitive nucleus and indefinite cytoplasm; (2) pigmentation by green chlorophyll, yellow carotenoids, the bluish phycocyanin, and sometimes the red phycoerythrin; (3) the photosynthetic product, sugar, and the storage of carbohydrates as glycogen; (4) the simple methods of multiplication, chiefly by cell division and fragmentation; (5) the three lines of development of form, starting from the single-celled types and culminating in the three types of colonies, irregular or spherical, square or cubical, and filamentous.

THE CHLOROPHYCEAE—GREEN ALGAE

GENERAL CHARACTERISTICS

The Chlorophyceae, or green algae, are characterized by their bright grass-green or yellow-green color. They form greenish scums on the

surface of quiet or stagnant water or grow firmly attached to submerged rocks, pieces of wood, and similar matter in swift-flowing streams or on lake shores. Many species of green algae also grow in the salt water of the ocean. Though most of them are aquatic, some grow in moist terrestrial habitats, such as moist soil and the shaded sides of rocks, trees, buildings, or old fences.

The green algae show a considerable range of variation in the form and structure of the plant body. Many of the lower members of the group are single-celled plants (Figs. 133, 134) or colonial forms. Of the unicellular plants, some are motile and some nonmotile. In the more advanced forms, nonmotile multicellular plants are the rule. Generally the plant body of the higher forms is a long filamentous structure, but sometimes it consists of a flat tissue-like expansion of cells (Fig. 146, A).

The protoplasts of the green algae are much better differentiated than those of the blue-green algae (Myxophyceae). Well-defined nuclei cytoplasm, chloroplasts, and, commonly, pyrenoids are present. The protoplast is generally surrounded by a cellulose wall which frequently attains considerable thickness. The nucleus is similar in all essential respects to that of the higher plants. Nucleoli and the chromatin reticulum are characteristically present. Nuclear division is by mitosis. The chloroplasts of many of these primitive forms are comparatively large and of various shapes. The chloroplasts contain the usual green and yellow pigments. For this reason, the Chlorophyceae are normally green plants, and are autotrophic, *i.e.*, they are capable of leading an independent existence. The process of carbohydrate manufacturing occurs in green algae as in higher plants, and there is no reason to suppose that it differs in principle. Carbon dioxide, being somewhat soluble in water, is available for photosynthesis. With water, carbon dioxide, and chlorophyll present, carbohydrates are formed. In many species the product of photosynthesis is stored as starch. Frequently starch accumulates around the pyrenoids. The pyrenoids are characteristically rounded bodies in the chloroplasts. They are thought to consist of protein centers surrounded by starchy layers. Pyrenoids seem to be related to nutrition, becoming prominent during periods of good nutrition and apparently disappearing during periods of starvation. The cells of these primitive plants apparently illustrate about the minimum structural equipment of a cell in any group of green organisms. But, after all, the cells in the most primitive organisms are not greatly different from those of the higher algae, and they in turn are not greatly different from the cells of plants considerably higher in the scale of development. Nucleus, cytoplasm, and chloroplasts are characteristic of all green algae.

Motile forms are provided with propelling structures known as *cilia*. The more primitive motile forms have several to many contractile vacuoles

and often a small colored plastid called an "eyespot" (Fig. 133). The cilia (singular, cilium), extending out from the anterior (front) portion of the cell, are slender hair-like processes often more than twice as long as the cell to which they are attached. By lashing the cilia, the cell propels itself through the water. The contractile vacuoles are regarded as reservoirs for the accumulation of waste materials of metabolism. By the contraction of the surrounding cytoplasm these waste materials are forced out through the cell wall. The eyespot is so called not because it is an organ of sight but because it seems to be sensitive to light, thereby enabling the organism to orient itself with respect to light.

Motility, a feature characteristic of organisms so low on the scale that they cannot with certainty be designated as plants or animals, is undoubtedly a primitive character. As the study progresses, it will be seen that this primitive feature—motility—is retained for reproductive structures occurring in all groups except in the highest division of the plant kingdom. Motility in reproductive cells finally disappears in the gymnosperms.

Asexual Reproduction. Most of the green algae increase in number by various nonsexual, or asexual, methods. Many of the simple one-celled kinds multiply through repeated cell divisions, each of which produces two daughter cells like the mother cell. In others, the numerous new cells cling together or are held together forming colonies. Sometimes, especially in the primitive colonial types, the vegetative structures may be broken up or fragmented, thus increasing their number. Besides simple fragmentation, special frequently motile single-celled structures, capable of growing into new plants like the parent, are formed. These special cells of various shapes and sizes, whether they possess some degree of motility or not, are called **spores**, or **gonidia**. A spore is generally a single-celled structure capable of growing and reproducing the plant. Spores are produced in diverse ways, but they have one feature in common, their formation by nonsexual methods within specialized cells usually called **sporangia**, or **gonidangia**. Asexual spores are produced without change of chromosome number. Thus each one is merely a vegetative piece of the parent plant, capable of duplicating it exactly. Numerous terms, indicating some structural or physiological feature, are applied to these asexual spores. If motile by means of flagella or cilia, the structure is called a **zoospore**. These motile spores are very common in most genera and are typical of green algae. The structure in which zoospores are produced is called a **zoosporangium**. Other names indicate their structural nature or manner of production. An **aplanospore** is a single, nonmotile spore produced within and separate from the wall of the vegetative cell in which it is formed. Another type, the **akinite**, is a spore in which the wall of the vegetative cell giving rise to the spore serves as the wall of the spore.

Sexual Reproduction. Most but not all green algae have methods of sexual reproduction which involve the formation of reproductive cells called **gametes**. If gametes are similar, without any distinction of sex, they are called **isogametes**; if they are different, with sex distinctions, they are **heterogametes**. In general, the sexual differences are expressed in size; the male gametes, or **microgametes**, are the smaller, and the female **megagametes**, or **macrogametes**, are the larger of the two kinds. Sometimes there are physiological sex differences in gametes of similar size. Sexual reproduction involving the fusion of similar gametes is called **isogamy**. When the fusion of heterogametes is involved, the process is **heterogamy**. Of the two types, isogamy is the more primitive, with heterogamy regarded as showing an evolutionary advance over the former. The structures in which gametes are produced are called **gametangia**. Thus the structure producing microgametes is the **microgametangium** and that producing the **macrogametes** the **macrogametangium**. In cases where sexuality is emphasized, equivalent terms, **antheridia** and **oögonia**, respectively, may be used. In these simple plants the **gametangia** are *single-celled structures*.

The Sexual Cycle in Algae. In order to function in sexual reproduction, gametes must fuse. Isogametes, although of similar size, probably differ physiologically and may be differentiated slightly as to sex. Thus the fusion of isogametes is a primitive sexual act. In heterogamous sexual reproduction in green algae, the larger gamete, or macrogamete, may be motile or nonmotile. The microgametes of green algae are generally motile and swim to the macrogamete, or egg. The fusion of gametes is called **syngamy**, or **fertilization**. The two gamete cells come together, their nuclei fuse into one, and the cell contents join, forming a single-celled structure, the **zygote**.

Associated with sexual reproduction is a change in chromosome numbers. Each species of organism has a characteristic number of chromosomes, with normally a definite number in each gamete. If the gametic number is designated as $1N$, fusion of two gametes will produce a zygote with $1N + 1N = 2N$ number of chromosomes. Actually, the sexual cycle is not completed until the $1N$ number of chromosomes is again restored. This is accomplished through a series of two specialized nuclear divisions called **meiosis** (pages 381 to 385). In most green algae, this process occurs in the zygote itself and for this reason is called **zygotic meiosis**. Zygotic meiosis, regarded as a primitive feature, usually results in the formation or maturation of four cells each with the $1N$ number of chromosomes. From one or more of these cells, frequently called **meiospores**, new plants are normally formed. In the algae, especially, the meiospores may develop cilia and exist for a period as motile cells.

Sexual reproduction with possibly motile cells developed as a final

product differs from all types of asexual reproduction because the fusion of gametes often from different parents provides possibilities of combining in one organism the traits of two parents. These combinations may offer the starting point for the development of new lines. Thus *the complete sexual cycle consists of the formation of gametes, their fusion at syngamy, the formation of a zygote, and the process of meiosis, which in most of the green algae occurs in the zygote itself.*

Origins and Evolution. The biological interest in the green algae lies in the primitive nature of the group. They represent many primitive structural features and methods of reproduction. While the present genera and species are probably not identical with the ancestors of the higher green algae, yet the simple plant bodies of the lower forms of the present day may be very similar to the kinds that appeared in early geologic periods. It is supposed that there was a common primitive stock from which all plant life has been evolved. It is possible that the complex and varied array of modern plants may have originated from relatively simple plants similar to some of the lower green algae. The motile single-celled forms and unspecialized colonial types are the ones generally regarded as points of origin of the higher green algae. Evolution is generally traced from the lower types into the filamentous forms.

The Classification of the Chlorophyceae, or Green Algae. The green algae are conveniently divided into numerous groups of ordinal rank of which nine are considered here:

Order I. Volvocales. Motile unicellular and colonial green algae, the latter not retaining capacity for cell division in the vegetative stages.

Order II. Chlorococcales. Nonmotile and colonial green algae not retaining capacity for cell division in the vegetative stages.

Order III. Tetrasporales. Nonmotile and colonial green algae retaining the capacity for cell division in the vegetative stages.

Order IV. Conjugales. The conjugating green algae.

Order V. Ulotrichales. The lower filamentous green algae.

Order VI. Chaetophorales. The heterotrichous green algae.

Order VII. Oedogoniales. Higher green algae. Motile reproductive structures have a "crown" of numerous cilia.

Order VIII. Siphonales. The tubular green algae.

Order IX. Cladophorales. The plant body divided into coenocytic cells.

ORDER I. VOLVOCALES

General Characteristics. The order Volvocales is of interest in that its members are primitive forms of aquatic plant life, showing the origin of many plant characters and life processes. All are motile, unicellular

or colonial plants, the colonies often of definite shape but never filamentous (Figs. 133 to 136). They are found more or less abundantly in inland fresh waters, particularly in quiet pools. The unicellular members of the group are of particular interest because they represent the most primitive of living green plants. It is believed that they are very similar to the forms from which green plants arose early in the earth's history. The vegetative forms assumed by members of this order are diverse, varying from single cells to colonies consisting of thousands of cells. A colony is a group of cells each physiologically independent of the others but mechanically held together generally in a gelatinous sheath. The features to be emphasized in the following discussion are (1) a consideration of their characteristics as primitive forms of plant life, (2) an almost perfect series of development in colony formation, and (3) the origin and development of sexual reproduction, coordinate in many respects with the series of colony forms.

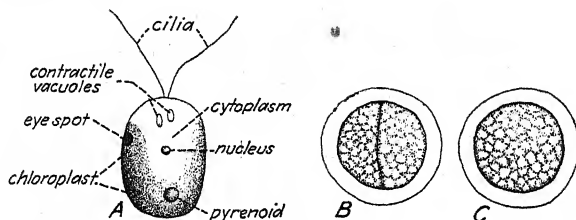


FIG. 133. *Chlamydomonas*. A, in vegetative condition; B, cell dividing; C, cell in resting condition. (Drawing by Chris. Hildebrandt.)

The Unicellular Volvocales. *Vegetative Form and Structure.* Of the several genera of the unicellular Volvocales, *Sphaerella* and *Chlamydomonas* are the most common and the best known. In both of these genera the cell is rounded, ellipsoid, or pear-shaped in outline, and motility is secured by means of two cilia of equal length and longer than the length of the cell, which project from the anterior end of the body (Figs. 133, 134). These cilia are observable without great difficulty in the living plant. West describes *Sphaerella* as having a central protoplast from which branched processes radiate outward, a cell wall extending around these processes, the outer part of the wall being a tough membrane and the inner portion of a mucilaginous nature. This twofold wall gives the organism the appearance of being surrounded by a sheath. *Chlamydomonas* does not have this sheathed appearance. Internally the cell structure of both genera is typical of that of all motile plant forms. A red eye spot is present, in addition to nucleus and cytoplasm, with the cup-shaped chloroplast located near the periphery of the posterior part of the cell. A pyrenoid and one or more contractile vacuoles are present. If the water in which

Sphaerella (Fig. 134) is growing evaporates, the organism goes into a prolonged resting period. In preparation for this, the cilia are retracted, the cell becomes spherical, the wall becomes thick, and a brick-red pigment colors the cell content. In this condition, the plant is easily recognized as a thin red film on the sides of old watering troughs, on damp soil, or in hollows in rocks. At high elevations in mountainous regions, the organism in this stage is frequently found forming a brick-red or purplish stain on the surface of snow where it has been blown from dried-out basins in the rocks. For this reason, *Sphaerella* has been designated as the "red snow alga."

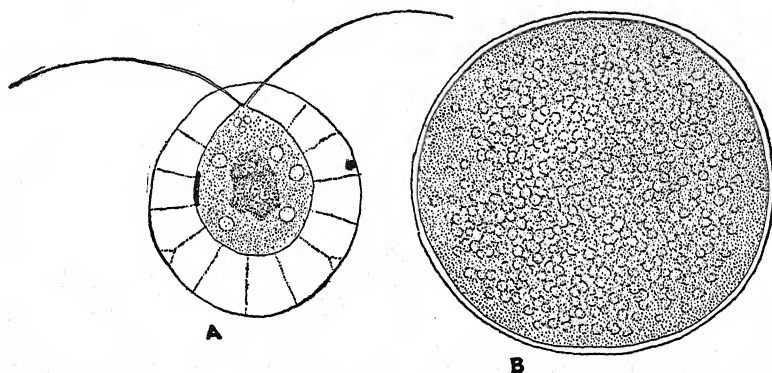


FIG. 134. *Sphaerella lacustris*. A, vegetative cell, showing the two cilia, the distended cell wall connected to the protoplast by cytoplasmic strands, the single (dark) eye spot, and five contractile vacuoles; B, cell in resting condition. (From Gilbert M. Smith, "Fresh-water Algae of the United States," Fig. 233, McGraw-Hill Book Company, Inc., New York, 1933.)

Asexual Reproduction. Increase in numbers, or asexual reproduction of such unicellular forms as *Chlamydomonas*, *Sphaerella*, and other genera takes place in two ways. In one type, the protoplast of the organism with all of its parts divides, and the whole cell, even in the motile stage, splits longitudinally. In the other type, multiplication takes place by division of the protoplast during a resting period, such as has been previously described. Following division of the protoplast, generally into two to four cells, the daughter cells still within the cell wall develop cilia and escape from it as motile cells. After enlarging into a mature cell, each represents the typical vegetative phase of the organism and may initiate a new life cycle.

Palmella Stages. Through a very generalized type of nonsexual multiplication accompanied by loss of motility of the individual cells, a temporary stage is sometimes developed by unicellular members of the Volvocales. This is the "palmella stage," so called because of its re-

semblance to the vegetative structure of the genus *Palmella* of the order Tetrasporales. In this condition, the individual cells are aggregated in loose colonies held together by a thin gelatinous sheath. Individual cells may retain their cilia, or flagella, but these become functionless and the cells are nonmotile. Rapid cell division in this stage increases the number of plants. After a period in this temporary palmella condition, the individual cells regain the use of their cilia and resume their customary motile existence. This feature is important because it represents a possible stage in the development of a permanent nonmotile condition of some members of order III, the Tetrasporales.

Sexual Reproduction. In the genera *Sphaerella* and *Chlamydomonas*, sexual reproduction also occurs. The cell content of a vegetative cell breaks up into a number of motile zoospore-like bodies that are, however, smaller and usually more numerous than the zoospores. Sometimes as many as one hundred of these bodies are formed within a single cell. They are known as **gametes**, though it is clear that they are only modified zoospores. These gametes differ from zoospores in that one gamete cannot by itself become a new *Sphaerella* or *Chlamydomonas* cell. Their union in pairs must precede further development. Since the uniting gametes are just alike, they are called **isogametes** (like gametes) and the process is **isogamous sexual reproduction** or **isogamy**. Some investigators, however, have reported finding gametes of unequal size in some of these unicellular forms. Like all sexual processes this is a fertilization process. The fusion of the protoplasts and nuclei of the two gametes constitutes the visible part of fertilization. The result of fertilization is a single cell called the **zygote**. The growth and development of this zygote into a heavy-walled resting cell may be thought of as the result of the stimulus of fertilization. Fertilization generally manifests itself in growth and development. The fusion of the gametes must, therefore, produce an influence or stimulation which expresses itself in growth. After a period of rest, generally covering a condition unfavorable for vegetative growth, the zygote germinates, *i.e.*, renews growth and activity. Germination in this case results in the production of several zoospores which escape from the containing wall of the mother cell and swim away as individual plants. This method occurs in both *Sphaerella* and *Chlamydomonas*.

The Colonial Volvocales. *Vegetative Form and Structure.* On the basis of their vegetative structure a number of genera of the colonial Volvocales may be arranged into a series with gradually increasing complexity. These forms are of singular interest and beauty. The series runs from the single motile cell described above, through colonies of 4, 8, 16 (Fig. 135), 32, 64, and 128 cells to the genus *Volvox* with thousands of cells (Fig. 136, A).

The culmination in size and complexity of the motile colony is reached in the genus *Volvox* (Fig. 136). The colonies of *Volvox* are spherical and, as microscopic organisms

go, are large. They are about the size of a small pinhead and consist of two thousand to fifty thousand cells. Each cell is a miniature of the *Chlamydomonas* type. The colonies of some species of *Volvox* show distinct protoplasmic connections between the cells, but this feature does not seem to be universal in all the species. The arrangement of the cells in a single parietal layer, resulting in a hollow spherical structure, is characteristic of *Volvox* colonies. The cells are definitely differentiated, only certain ones taking part in reproduction.

Asexual Reproduction. The asexual reproduction of the colonial forms differs from that of the unicellular forms in that the vegetative cells divide, forming zoospore-like bodies that cohere within the parent cell to form a new colony, the whole mass being retained for some time in the original sheath of the colony. This results in the formation of a group of young daughter colonies held within the sheath of the mother colony. In the more simple and primitive members of the colonial Volvocales, every

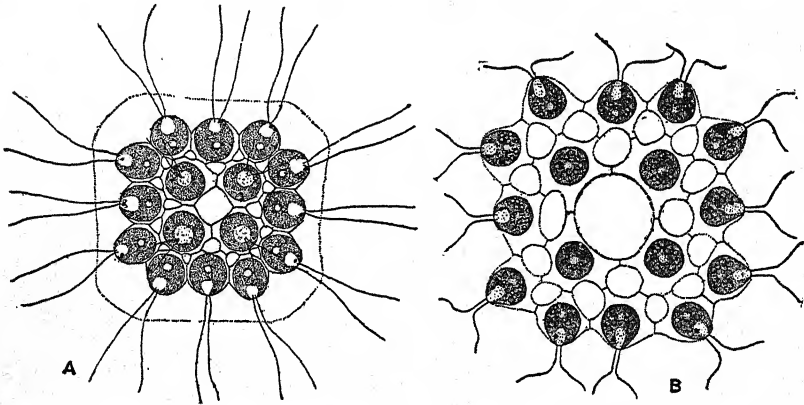


FIG. 135. A, *Gonium pectorale*; B, *G. formosum*; 16-celled colonies, each cell biciliated and imbedded in a gelatinous matrix. (From Gilbert M. Smith, "Fresh-water Algae of the United States," Fig. 223, McGraw-Hill Book Company, Inc., New York, 1933.)

cell of the colony divides thus to form a new colony, and the division results in the formation of the number of cells characteristic of the number of cells in the colony of the species in question. For example, there are two species of *Gonium*, one with 4 cells in each colony and the other with 16 cells in each colony (Fig. 135). When these reproduce asexually, each cell of the species having 4 cells in the colony divides into 4 cells, forming in that way 4 new colonies of 4 cells each. In the species having 16 cells in each colony, each cell divides into 16 cells, thus forming 16 daughter colonies each containing 16 cells. Eventually, the colonies escape and swim away.

In the genus *Volvox* the highest development of the order is reached, where the method of asexual reproduction is somewhat different. Only a few, generally from one to a dozen, of the thousands of cells of the colony take part in asexual reproduction. A vegetative cell enlarges and gradually pushes back into the colony. Soon division begins to take place within the enlarged cell and continues forming new cells until a considerable number are formed (Fig. 136). The cells of the daughter colony are retained within the cell wall of the dividing mother cell. This cell wall forms the beginning of the retaining gelatinous membrane surrounding the young *Volvox* colony. The number of cells in the daughter colony is apparently indefinite. Usually there

are several young daughter colonies forming simultaneously in the mother colony. Often they remain within the mother colony until they have attained considerable size, as much as one-fourth the diameter of the mother colony, before escaping. During the period in which the daughter colonies are held within the mother colony, they float free within the hollow portion of the colony. Eventually the young colonies escape by the rupture of the membrane of the mother colony.

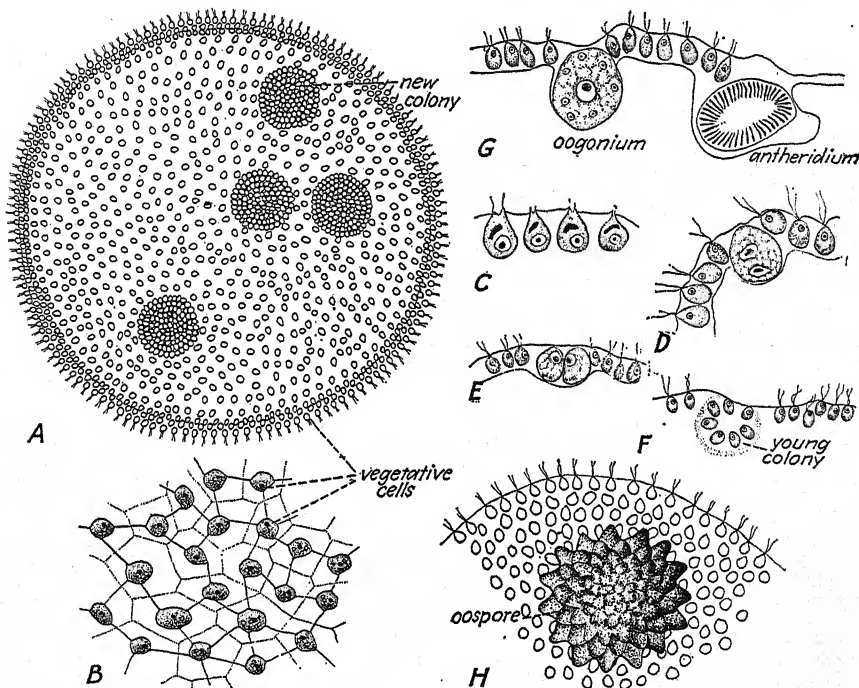


FIG. 136. *Volvox*. A, vegetative colony with four younger colonies; B, a portion enlarged, showing coalescent sheaths and cytoplasmic connections from cell to cell; C-H, sections of portions of colonies; C, vegetative cells; D-F, beginning of asexual reproduction by formation of new colonies; D, vegetative cell enlarged; E, cell similar to D after the first division; F, further divisions to form young colony within parent colony; G, showing antheridium containing sperms, and oögonium containing egg; H, the warted oöspore resulting from fertilization of the egg by a sperm. (A, B, and H by Helen D. Hill.)

Sexual Reproduction. In the genus *Volvox*, sexual reproduction has attained high-grade **heterogamy**. The gametes are sharply differentiated, the female gametes, or eggs, being nonmotile and very much larger than the male gametes, or sperms, which are motile. In some species, the sexes are further separated by a dioecious condition of the colonies, or the occurrence of distinct male and female colonies. However, in other species, the colonies are monoecious, both male and female gametes being produced in the same colony. When the gametes form, certain cells of the colony enlarge to become **gametangia** (cells containing gametes) (Fig. 136, G). In the case of the formation of male gametes, the cell content divides many times, forming a large number of small cells, becoming eventually the sperms, which are very small

and motile. The cells which are to form the female gametes or eggs do not divide. These cells enlarge to many times the size of an ordinary vegetative cell, and the entire protoplast of each becomes an egg cell. When mature, these eggs are fertilized by the sperms, a single sperm fusing with each egg cell. These fertilized eggs develop heavy spiny walls and become the zygotes (Fig. 136, *H*). After a period of rest the content of each zygote develops a new colony which escapes from the cell by rupture of the wall and swims away.

Significance of the Volvocales. Primarily, there is interest in algae because they are a primitive group and represent a possible basis for the evolution of all green plants. Forms like *Chlamydomonas* are significant because they show the cell structure of primitive unicellular plants. The chlamydomonine cell particularly has been studied because it is regarded as basic in the evolution of vegetative structures. It is thought that with notable modification this type of cell has been adapted to existence in the higher forms. Evidence in support of this idea is found in the frequent reversion of the reproductive cells of the higher algae to the chlamydomonine type during their motile stages.

Evolutionary Trends in Volvocales. The Volvocales show some of the most complete evolutionary series known. With scarcely a break in the stages of development, *Chlamydomonas*, *Spondylomorom*, *Gonium*, *Pandorina*, *Eudorina*, and the complex *Volvox* show a series of colonial structures all retaining the primitive feature of motility. Of similar interest is the evolution and development of sexual reproduction paralleling that of vegetative colonies in this group. The lower forms of the Volvocales like *Gonium* and *Pandorina* have isogamous reproduction with here and there a tendency toward the production of unlike gametes. Heterogamy is definitely established in *Eudorina* and highly developed in *Volvox*.

Summary of the Volvocales. The Volvocales, a group of primitive, actively motile algae, have ciliated cells consisting of a thin wall or membrane and protoplast with definite nucleus and cytosome. The cytosome contains a cup-shaped chloroplast and frequently a red-colored eyespot, all cytoplasmic in nature. This kind of cell is known as the chlamydomonad or chlamydomonine type. Increase in numbers occurs by vegetative cell division in the lower single-celled forms of the order. In the higher forms, the vegetative cells are aggregated into colonies, or coenobia, of definite shapes. In asexual reproduction in colonial types, several or all vegetative protoplasts divide into the number of cells characteristic of the colony in that species. Sexual reproduction ranges from isogamy to heterogamy with the production of resting zygotes. New colonies are formed by division of the protoplast of the zygote.

ORDER II. CHLOROCOCCALES

General Characteristics. The order Chlorococcales is an assemblage of mostly fresh-water algae with diverse size, organization, and shape. Some members of the

group are single-celled plants; some are organized into small colonies of very definite shape and size; others form large colonies. They occur often as free-floating but nonmotile organisms, but some of the smaller types grow attached as epiphytes on other algae and on larger water plants. Some, but not all, of the algae existing as endophytes within the bodies of such living animals as *Paramecium*, fresh-water sponges, and others belong to this group.

One member of the Chlorococcales, the genus *Chlorella*, has come into prominence recently as a source of the antibiotic *chlorellin*, which is being investigated in the control of bacterial disease. It may be recalled that increase in cell numbers occurs regularly through cell division in the motile vegetative and the palmella stages of

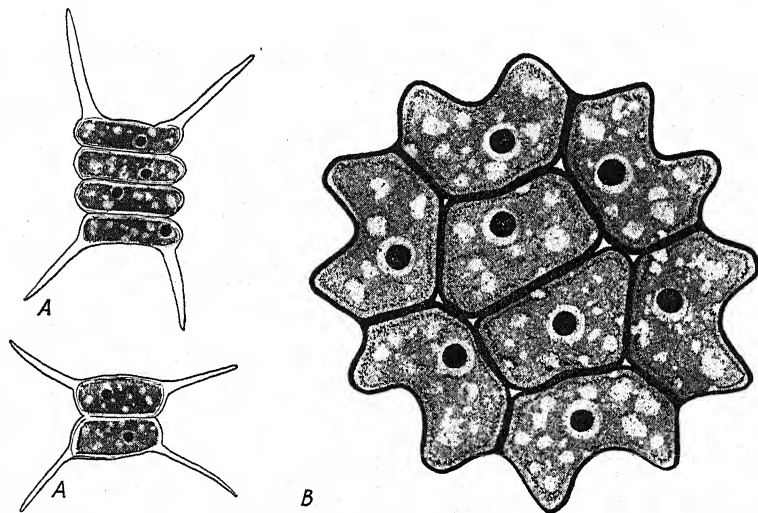


FIG. 137. A, *Scenedesmus*, two- and four-celled colonies, with stout spine-like appendages on the terminal cells; B, *Pediastrum*, eight-celled colony.

Chlamydomonas and other unicellular Volvocales. This feature is lost or limited in the highly specialized colonial forms. In the course of their evolution, the loss of this capacity by the Chlorococcales is a limitation on size in most of the order. In many of the genera, the form and special features of the colony are definitely fixed (Figs. 137, 138). In the vegetative plant body in the Volvocales, motility is universal, even in the large and complex *Volvox* colonies. None of the Chlorococcales is motile in the vegetative stage, but the reproductive structures such as zoospores and gametes are characterized by motility. Besides *Chlorella* there are about 90 other genera of the Chlorococcales. Of these, *Scenedesmus*, *Pediastrum*, and *Hydrodictyon* are well known and may illustrate some of the important features of form, organization, and life cycles in the order (Figs. 137, 138).

Scenedesmus. *Scenedesmus* is a microscopic plant consisting of two to four, rarely more, elongated cells arranged parallel in a nonmotile colony. Multiplication occurs when the protoplasts of vegetative cells divide into the number of nonmotile cells characteristic of the colony. These, remaining attached, escape from the mother cell as a new colony. No sexual reproduction is known in *Scenedesmus*.

Pediastrum. *Pediastrum* occurs in flat radiate colonies, or coenobia, with 4 to 128 cells. Colonies of 16 cells are common. The word *astrum*, meaning star, refers to its

radiate form. Nonsexual reproduction takes place by motile cells formed by division of the protoplasts of the cells of the colony. Multiplication is individual for each cell, not simultaneous for all cells of the coenobium as, for example, in the volvocine *Pandorina*. As in *Pandorina*, the number of zoospores formed in each cell is that characteristic of the colony. After division of the protoplast, the zoospores enclosed in a thin retaining membrane escape from the mother cell. The zoospores swim around inside the sac-like structure for a very short time, arrange themselves in the position of the cells in the parent colony, and suddenly become motionless. The cells then grow to normal adult size.

Hydrodictyon. *Hydrodictyon* is a large macroscopic alga. The word *dictyon* means "net"; thus as the name implies, the vegetative plant body grows as a net-like structure usually floating on the surface of quiet fresh waters. While this alga is not very common, when it occurs it may be very abundant. Young cells contain a single

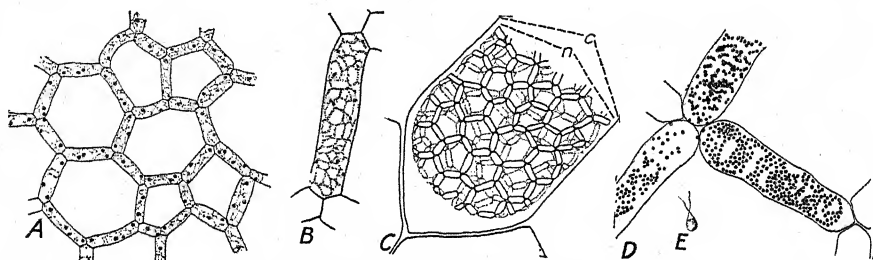


FIG. 138. *Hydrodictyon*. A, small portion of the sac-like net characteristic of the "water-net" alga, the cells all in vegetative condition; B, single cell from a vegetative net enlarged, showing pyrenoids and chloroplasts; C, portion of a cell, c, from a net showing a young net, n, within, formed by the conjoining of zoospores; D, three cells from a net showing isogametes within the cells; E, a single gamete. (Drawings by Helen D. Hill.)

nucleus and a single pyrenoid, but older cells become multinucleate coenocytes with a large reticulate chloroplast containing many pyrenoids. Pyrenoids and nuclei may be distinguished by their size, the former being larger. Multiplication occurs when the protoplast of the vegetative cells divides to form large numbers of very small zoospores which swim within the parent cell. The zoospores come to rest and arrange themselves as the meshes of a new net, which is eventually freed by disruption of the old cell wall (Fig. 138).

Sexual Reproduction. Sexual reproduction is similar in *Pediastrum* and *Hydrodictyon*. In each of these algae the protoplast of the vegetative cell divides into isogametes, which are formed in the same manner as the zoospores. Gametes are very much smaller and more numerous in the cell than zoospores. They escape through the cell wall and fuse in pairs to form zygotes, which after a period of rest undergo division, forming four motile cells that escape from the zygote wall. These soon lose their motility and develop unique structures of peculiar polyhedral shape unlike anything else known in algal life cycles. The *polyhedra* develop thickened walls and become resting cells. Upon germination the protoplasts of the polyhedra undergo division into small nonmotile cells which arrange themselves into the typical form of the species. In the case of *Pediastrum*, a new flat disk-shaped plant is formed, and in *Hydrodictyon* a new net is formed within the wall of the *polyhedron*.

Evolution in the Chlorococcales. Colony formation is a feature of the higher members of the Chlorococcales. *Scenedesmus*, *Pediastrum*, *Hydrodictyon*, and many

others are colonial types. Development of colonies in the Chlorococcales parallels that in the Volvocales but here they are strictly nonmotile in the vegetative phases. These plants, however, show greater adaptability to environment than the Volvocales, as evidenced by their diverse habitats. They live free floating, epiphytic, and endophytic. The Chlorococcales, while exhibiting considerable structural development in the vegetative phases, failed to evolve sexually beyond the stage of isogamy.

Summary of the Chlorococcales. The members of the Chlorococcales range in size from simple one-celled plants to extensive floating colonies. Most of the colonies are of very definite shapes and of limited sizes. Because of the loss of capacity for division in vegetative cells, there is no increase of vegetative cells after the colony is formed. Asexual reproduction is by formation of definite numbers of motile cells from the protoplasts of vegetative cells in the colony. These promptly organize a new nonmotile colony. Isogamous sexual reproduction occurs in many forms of the Chlorococcales. Fusion of gametes produces the zygote. Motile cells from the zygote introduce peculiar nonmotile thick-walled resting cells of irregular shapes called polyhedra. Eventually, typical vegetative colonies are formed within the polyhedral wall by division of the protoplast.

ORDER III. TETRASPORALES

General Characteristics. The algae belonging to this group are one-celled nonmotile green plants growing singly or in loose colonies. Among those growing singly, although simplicity is a general feature, there are slight diversities in cell form. Some kinds, such as *Tetraspora* and *Palmella*, occur in extensive gelatinous colonies growing in quiet fresh waters. The vegetative cells of *Tetraspora* have functionless cilia, or flagella, but those of *Palmella* have no cilia.

The typical vegetative condition in these genera resembles the temporary "palmella stage" occasionally found in the unicellular members of the Volvocales. For this reason, the two orders are thought to be closely related. Origin of the Tetrasporales from the lower members of the Volvocales might have occurred as the temporary palmella stage of the latter became fixed as the normal vegetative form with permanent loss of motility of the individual vegetative cells. The presence or absence of cilia and the features of motility and nonmotility are hereditary traits which may have arisen as variations or mutations and become permanently changed characteristics. In this way, new forms may originate. Because of their evident close relationships, the two groups have sometimes been considered as motile and nonmotile families within one order, the Volvocales. The genus *Tetraspora*, as its name indicates, is characterized by the occurrence of its vegetative cells in groups of four (Fig. 139, A). A single vegetative cell undergoes two successive divisions and forms four daughter cells, which remain close together, possibly because of the physical nature of the gelatinous matrix in which they are embedded. Besides the loose gelatinous palmella type of colony, some genera of the Tetrasporales form branched, dendroid, or tree-like, colonies frequently of definite shapes. Still other kinds grow as single organisms attached as epiphytes on larger aquatic plants.

Asexual Reproduction. Colonial forms in the Tetrasporales may be increased and disseminated by fragmentation of the colonies. In forms like *Tetraspora* and *Palmella*, this may occur through breaking up of the fragile gelatinous mass of the colony. Most of these plants multiply by simple division of the cells. In this way, colonies may originate from a single cell, and after it is once started, the mass of the colony may be rapidly increased until it contains thousands of cells. Retention of the capacity for unlimited cell division and growth during the vegetative phase is basic to

the extensive development of these large unspecialized colonies. This capacity, evidence of their primitive plastic nature, is a highly important feature of the Tetrasporales. Asexual reproduction by means of zoospores formed two to four within the walls of the mother cell is common among the Tetrasporales. When this occurs, the motile spores escape from the original cell, come to rest, and later form new colonies.

Sexual Reproduction. Sexual reproduction has been studied in a few of the Tetrasporales. Two, four, or eight gametes of equal size are formed by division of the protoplast in a vegetative cell. Colonies may be dissimilar as to sex, some producing male and other female gametes although there is no difference in their size. Sexual reproduction is therefore anisogamous. The zygote germinates, forming probably four, possibly eight, nonmotile cells which start new colonies.

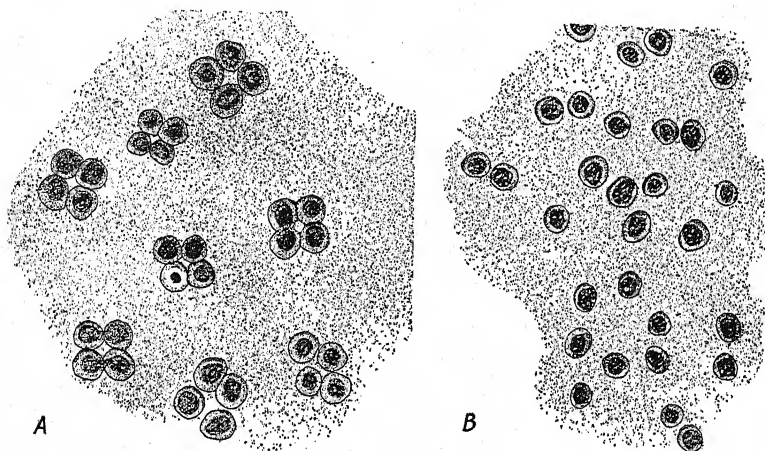


FIG. 139. A, *Tetraspora*; B, *Palmella*; both showing cells imbedded in a gelatinous matrix with *Tetraspora* showing typical grouping of four cells. (Drawing by Helen D. Hill.)

Summary of the Tetrasporales. The members of this order are very similar to the unicellular Volvocales except that they lack motility. An important feature is the retention of capacity for vegetative cell division. Increase in number of individuals is by division of the vegetative cells. Asexual reproduction takes place by formation of two to four zoospores in a vegetative cell. Sexual reproduction occurs by fusion of isogametes to form zygotes. Germination of the zygote takes place by division of the protoplast into a few cells which start new colonies.

ORDER IV. CONJUGALES

General Characteristics. The members of this order constitute a very definite group of the green algae. They are all strictly fresh-water plants of fairly wide distribution. In the group are some of the best known genera of all the algae. Species of the genus *Spirogyra*, although in many respects not typical of the green algae, are almost universally studied in elementary laboratory courses in botanical science. The outstanding features of the order are (1) a total lack of motility, even the reproductive cells being nonmotile; (2) the large, definitely shaped chloroplasts char-

acteristic of the various genera; (3) general lack of definite asexual methods of reproduction; and (4) a low-grade isogamous sexual reproduction of an unusual type known as conjugation. This last character furnishes the basis for the descriptive name of the order—Conjugales. The total lack of motile reproductive cells is an unusual and striking condition in a group of aquatic plants in which motility is normally expected. Such a complete lack of motility is found in but two other groups of algae, the Rhodophyceae, or red algae, and the Myxophyceae, or blue-green algae. The order Conjugales is divided naturally into two families on the basis of the unicellular or multicellular structure of the plants. The unicellular Conjugales with many genera and hundreds of species are grouped in the family Desmidiaceae. The multicellular, filamentous species are included in less than 10 genera in the family Zygnemaceae.

Unicellular Conjugales (Desmidiaceae). *General Features.* The members of the Desmidiaceae are collectively known as **desmids**. They are single-celled, nonmotile plants of very diverse form and rare beauty but are particularly characterized by the fact that the cells are usually divided into two symmetrical halves by a median constriction (Fig. 140). The two halves are referred to as **semicells**; the constriction is called the **sinus**; and the narrow portion connecting the two halves is known as the **isthmus**. The cell wall consists of two layers, an inner one of cellulose and an outer one of cellulose impregnated with other materials, frequently iron. Numerous small pores occur in the cell wall and through these an enveloping mucus or mucilaginous material is extruded. The margins of the cell wall are lobed, indented, or have other diverse patterns. When observed from the end view, the cells are often triangular in outline and frequently show radiating processes. The diversity of the forms of the desmids is so great that it is impossible in a brief discussion to describe the various genera adequately.

Cell Structure. The cell structure is very diverse. In general, the cell consists of the much sculptured wall, the protoplast with its nucleus, cytoplasm, one or two chloroplasts, and one or more vacuoles (Fig. 141). Most of the desmids have a single nucleus, located centrally, and two relatively large chloroplasts, one located in each semicell. The nucleus is embedded in a small mass of cytoplasm and in the case of constricted forms is located in the isthmus. The remainder of the cytoplasm is variously disposed in the cell. The chloroplasts are provided with pyrenoids which are frequently numerous.

Growth, Cell Division, and Asexual Reproduction. Growth, cell division, and asexual reproduction are intimately associated and may in fact all be considered as different phases of the same process. Of the two semicells that constitute the desmid plant, one is always younger than the other. The younger semicell is at first very small, but it gradually attains the same size as the other semicell. This feature is due to the manner of cell division. When the desmid divides, the nucleus undergoes division first. The isthmus where the nucleus is located elongates and a constriction forms on the isthmus wall between the two new nuclei. At this constriction, a wall is laid down across the isthmus. Each half of the isthmus then begins to enlarge and grows into a new semicell the size of the old one. A new chloroplast is formed in each of the new semicells which soon separate at the point of contact, and asexual multiplication is accomplished (Fig. 141).

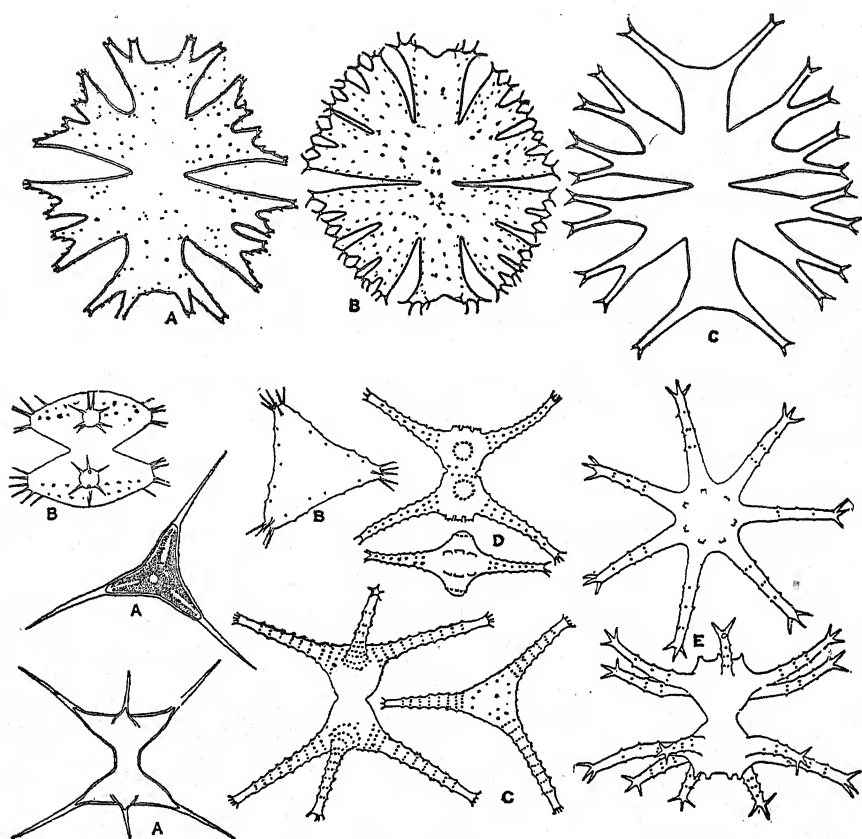


FIG. 140. Various forms of desmids. Upper row, A, B, C, species of the genus *Microsterias*; lower series, A-E, species of *Staurastrum*. (From Gilbert M. Smith, "Fresh-water Algae of the United States," Figs. 406 and 408, McGraw-Hill Book Company, Inc., New York, 1933.)

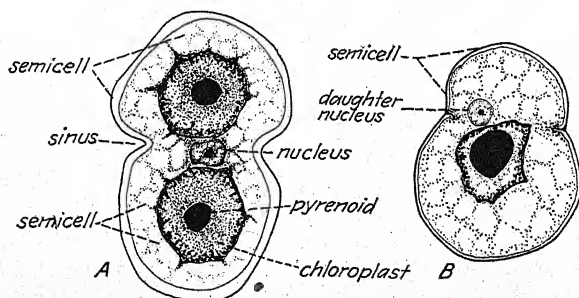


FIG. 141. *Cosmarium*. A, cell before division, showing the two semicells, the sinus, the centrally placed nucleus, and the large chloroplasts in semicells, each chloroplast containing a single pyrenoid; B, one semicell of the original cell and a new semicell growing from the region of the sinus; the single nucleus of the parent cell has divided, leaving a daughter nucleus for the new cell; other parent semicell not shown.

Sexual Reproduction. Sexual reproduction in desmids is by **conjugation**, a process of isogamous reproduction in which two entire cell contents behave as gametes. The cells which are to conjugate come together and generally become embedded in a common mucilaginous mass. The cells open at the isthmus, the semicells separating and allowing the protoplasts to emerge. Each protoplast acts as a gamete. They come together and fuse, forming a zygote which surrounds itself with a heavy wall, frequently covered with spines, warts, or other outgrowths (Fig. 142). The walls of the four empty semicells, being held together by a gelatinous envelope, frequently remain near the newly developed zygote. Fusion of the nuclei of the two protoplasts, although delayed, takes place eventually, and fertilization is accomplished. After a period of dormancy, the zygote or zygospore germinates by the production of two or more young desmid plants. Sexual reproduction in the desmids is more rarely observed than in the filamentous Conjugales.

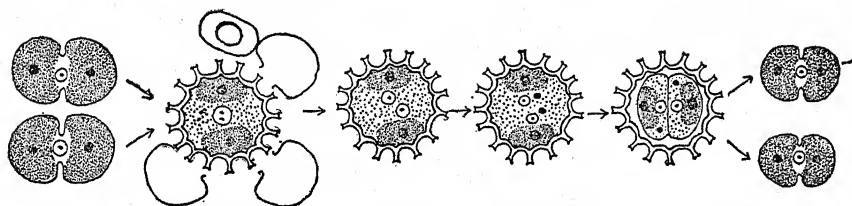


FIG. 142. Diagram to show conjugation and the germination of the zygote of a species of *Cosmarium*. Explanation in the text. (From Gilbert M. Smith, "Fresh-water Algae of the United States," Fig. 395, McGraw-Hill Book Company, Inc., New York, 1933.)

Filamentous Conjugales (Zygnemaceae). *General Features.* The members of this family are usually unbranched filamentous plants. Instances of branching have been reported but the branches are never well developed. The filament is composed of cylindric cells growing end to end. Most species grow unattached in quiet water in thick free-floating masses, but a few species have holdfasts attaching the filaments to stones and other objects in the shallow water where they thrive. *Spirogyra* is probably the best known genus.

Cell Structure. The cylindrical cells composing the filaments are in general alike in all the genera, with slight differences in the disposition of the parts of the cell due to the nature of the chloroplasts. The cells of the several genera and species vary in size. Each cell consists of a cell wall, and a protoplast, with its nucleus, cytoplasm, and one or more chloroplasts. In *Spirogyra* the center of the cell is occupied by one or more vacuoles. The chloroplasts of all species are large and conspicuous and are beautiful objects when viewed with a microscope. Each chloroplast has from one to several prominent pyrenoids.

Spirogyra, *Zygnema*, and *Mugeotia*, the principal genera of the family, illustrate the forms of chloroplasts found in the group (Fig. 143). The chloroplasts of *Spirogyra* are in the form of spiral bands that are wound around the outer portion of the protoplast just inside the cell wall.

The edges of the ribbon-like chloroplasts are often scalloped. Pyrenoids are present in each chloroplast. The nucleus is generally located in the center of the cell and is embedded in a mass of cytoplasm, from which radiating strands pass to the region of the pyrenoids in the chloroplasts. The chloroplasts of the cells of *Zygnema* are radiate, or star-shaped, two in each cell, centrally placed, with the nucleus embedded in a mass of cytoplasm suspended between them. The chloroplast of *Mugeotia* is a single flat band in axile position in the cell.

Growth, Cell Division, and Asexual Multiplication. Growth and cell division are not restricted to any particular part of the filament. Cell division is preceded by division of the nucleus. Division of the chloroplasts normally follows that of the nucleus. The new cell wall is then formed as a ring-like growth which gradually approaches the center of the cell and finally separates the chloroplast and the cytoplasm into two equal parts (Fig. 143).

The Zygnemaceae are deficient in methods of asexual reproduction. Aplanospores are formed in some instances. In this process, which is purely asexual, the contents of a cell round up, develop a heavy cell wall, and form the **aplanospore**, which is a resting spore. Each aplanospore upon germination produces a new plant. Multiplication by means of fragmentation, the filaments breaking at the walls where the cells join together, is said to be common in *Spirogyra* but rather rare in other genera.

Sexual Reproduction. Sexual reproduction in the genera of the Zygnemaceae is accomplished by **conjugation**, an isogamous method, which is characteristic of the order Conjugales. In the process, two vegetative cells combine their contents to form a zygote. In *Spirogyra* (Fig. 143, B) this fusion of cell contents takes place within one of the two conjugating cells; in some forms it occurs midway between the two participating cells. In either case, the gametes are formed from the undivided protoplasts of vegetative cells. Conjugation may occur between cells of two adjacent filaments or, much more rarely and restricted to certain species, between two adjacent cells of the same filament. In the former case, two parallel filaments lie adjacent to each other, the cells touching at various points. Short tube-like projections develop from two opposite cells at these points of contact. By further growth of these tubes the filaments are gradually pushed apart, but the ends of the tubes remain attached. Soon the end walls of these coalesced tubes are resorbed and a continuous passageway is left between the two cells or gametangia. Thus the conjugation tube is formed.

In *Spirogyra* and sometimes in *Zygnema* the contents of one cell pass through the conjugation tube and fuse with the contents of the other cell (Fig. 143). The cell furnishing the migrating gamete is regarded

as the male gametangium, producing the male gamete, and the receiving cell the female gametangium, producing the female gamete. This type of reproduction, despite the slight difference in the gametes, is considered isogamous, since there are no other visible differences between them.

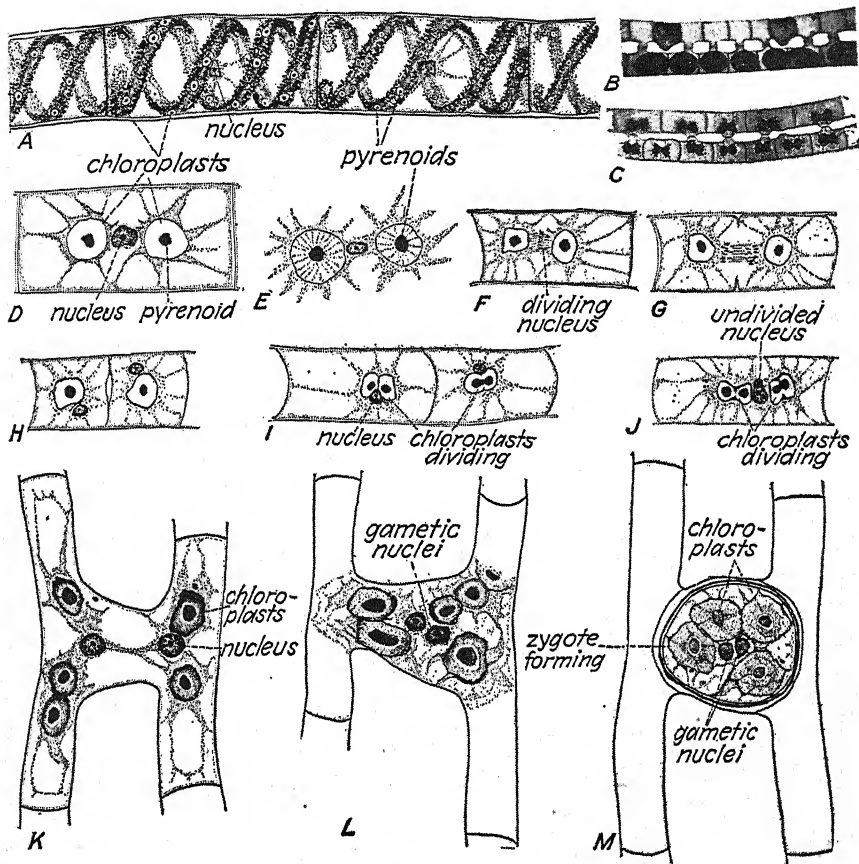


FIG. 143. Filamentous Conjugales. A, portion of a vegetative filament of *Spirogyra*; B, *Spirogyra* conjugating, showing dark, ellipsoid zygotes; C, *Zygnema*, early stage of conjugation; D-J, *Zygnema*, details of cell structure and cell division; D, vegetative cell; E, structure of the plastids; F-I, normal cell division, plastid division following nuclear division; J, abnormal division, plastid division preceding nuclear division; K-M, *Zygnema* species, zygote forming in the conjugation tube.

Generally all the cells of a filament behave in the same manner in this respect, becoming either all male or all female gametangia. Rarely gametes of both sexes are found in the same filament. Occasionally several parallel filaments are joined in conjugation, the filaments alternating with respect to the sex of the gametes. When adjacent cells of

the same filament conjugate, it is called lateral conjugation, but generally conjugation is between the cells of two filaments. Where lateral conjugation occurs, this indicates that the filament is monoecious, *i.e.*, contains cells of both sexes.

After the gametes come together in one of the gametangia or in the conjugation tube, they fuse, forming a zygote. The fusion of the nuclei is frequently considerably delayed. The chloroplasts contributed by the male gametangium are said to disintegrate, but those from the female persist in the zygote. Fertilization here as elsewhere has two results, a doubling of the amount of chromatin and the number of the chromosomes and a stimulus to growth. The stimulus to growth expresses itself in this case in the maturing of the zygote. The zygotes (Fig. 143), ellipsoid or spherical in shape, are provided with a heavy wall and rest for some time, generally over a period unfavorable to growth. Upon the return of proper conditions for growth, the zygote germinates and produces a new filament directly. Meiosis, which reduces the amount of chromatin one-half and the number of chromosomes to one-half the number, takes place at the first division of the nucleus of the zygote.

Summary of the Conjugales. The order Conjugales is composed of two families separated on the basis of structure. The family Zygnemaceae includes multicellular filamentous plants, and the family Desmidiaceae unicellular plants of distinctive appearance. The relatively large and distinctive chloroplasts are the outstanding feature of the cell structure of members of the order. The total lack of motile reproductive bodies, a negative feature, is the chief characteristic of the reproduction. A corollary to this is the method of sexual reproduction, which is by the conjugation of large nonmotile isogametes. The germination of the zygotes directly to form new plants is also a characteristic feature of the members of this order.

ORDER V. ULOTRICHALES

General Characteristics. The members of the more than 60 genera in the order Ulotrichales may well be regarded as the typical green algae. They are fresh-water algae which grow under very diverse conditions. Some occur in cold running water; some in quiet water; others are epiphytic upon larger water plants; a few grow within the tissues of other plants. Most species are attached to some sort of substratum. They show considerable diversity of form, ranging from unbranched filaments to predominantly branched filaments, and in a few species the plant body is a discoid thallus. In many genera, slight cell differentiation occurs in the modification of the basal cell to form a holdfast, attaching the plant to its substratum. Otherwise, the cells of the filaments are usually all nearly

shows an evolutionary advance in vegetative form. The alternation of haploid and diploid forms is unusual and important.

ORDER VI. CHAETOPHORALES

General Characteristics. The members of this order have two types of vegetative filaments, which may be branched. One of these filaments grows prostrate and the other erect. This condition is referred to as **heterotrichous**. *Chaetophora* (Fig. 145) and *Draparnaldia* are simple members of this order. Their branching habit may be regarded as indicating an evolutionary advance over the simple unbranched filamentous species. In other points, however, species of these genera show only relatively slight variations from the condition found in *Ulothrix*. Asexual reproduction by zoospores and sexual reproduction by small motile isogametes are features common to all three genera.

In the genus *Coleochaete* the plant body is a small flat disk-like thallus usually consisting of a single layer of cells (Fig. 146, A). The size of the thallus varies with the species, from less than 1, to 2 or 4 mm., but generally it is about the size of a pinhead. In some species, the thallus is not so well developed and consists of scarcely more than a series of closely associated radiating filaments all lying in one plane. Asexual reproduction is by zoospores. These structures are produced singly in certain cells of the thallus, which become the zoosporangia. The zoospores of *Coleochaete* are larger than those of *Ulothrix*. Sexual reproduction shows a considerable advance over other members of the order. Sexual reproduction is heterogamous. It is this feature, together with the thallose body of *Coleochaete*, which justifies its position as perhaps the highest type of green alga. Usually the gametes are produced in gametangia (Fig. 146, C-E) of different sizes and sometimes on different plants (dioecious). The male gametes (sperms) are produced, few, often only one, in a male gametangium (antheridium). Each male gamete is biciliated and either colorless or possessing a green chloroplast. At maturity, they escape from the antheridium and swim to the oögonium. The oögonium produces a single female gamete (egg), which has a single green chloroplast. The oögonium is provided with a beak-like projection, called the **trichogyne**, which functions to receive the sperm. When the oögonium is mature, the trichogyne opens, and the sperm penetrates to the egg

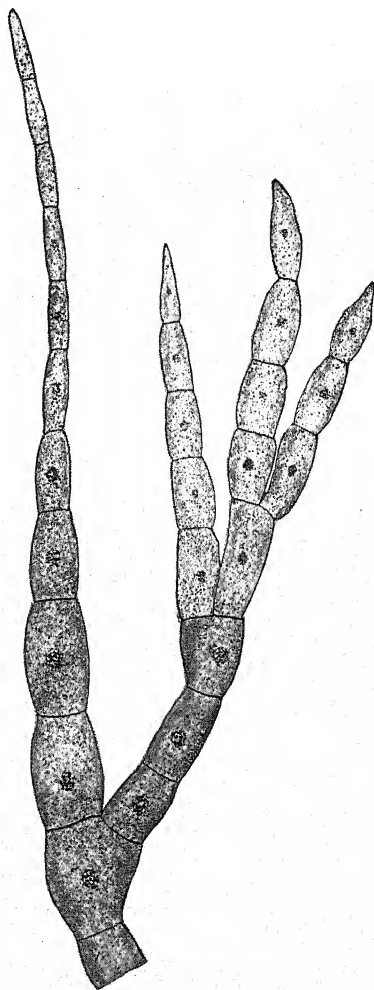


FIG. 145. Branched filament of *Chaetophora*.

where the nuclei of the two gametes fuse and thereby accomplish fertilization. In this genus, fertilization of the egg within the oogonium is followed by a development unusual for the green algae. The fertilized egg, or zygote, develops a heavy wall and the entire oogonium becomes completely covered by an overgrowth of the surrounding vegetative cells of the thallus. This structure turns brown and goes into a resting period. Upon germination, the protoplast of the fertilized egg undergoes a series of divisions, developing a mass of cells within the wall of the zygote. Each cell of this mass finally develops into a new plant.

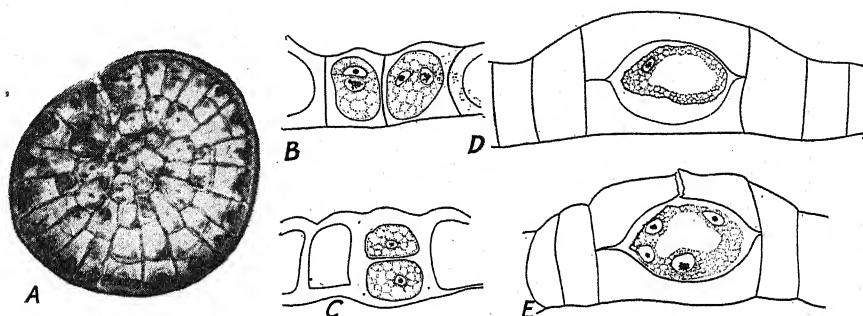


FIG. 146. *Coleochaete*. A, vegetative plant body consisting of a flat plate of cells; B-E, cross sections of thallus; B, vegetative cells; C, antheridium; D and E, oogonia.

Protococcus. One of the most widely distributed of all algae is a small form, *Protococcus*, or *Pleurococcus* (Fig. 147). This alga grows in moist locations on trees, old fences, stone walls, and similar situations. Usually the plants are single spherical cells, occurring either as isolated individuals or in small, compact masses or groups consisting of three or more cells. These masses can scarcely be designated as colonies since they are the result of incomplete separation of the cells following division. Individual cells are generally small and have heavy cellulose walls, a single nucleus, and a relatively large dense chloroplast. Nucleus and chloroplast are often difficult to distinguish as definite bodies without special staining.

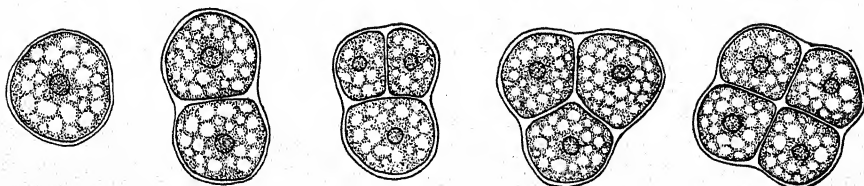


FIG. 147. *Protococcus*. Single cell and cells united in colonies of two, three, and four, each cell showing a nucleus and vacuolate cytoplasm.

Occasionally when submerged or growing under very moist conditions and perhaps under certain physiological conditions, *Protococcus* forms short filaments consisting of three or four cells as in small *Ulothrix* or *Chaetophora* plants. On the basis of cell structure and the infrequent development of simple vegetative filaments, *Protococcus* is thought to be more closely related to forms like *Chaetophora* than to any other algae. It is thought that it was originally a filamentous form in which both vegetative structures and reproductive functions have retrogressed, for apparently *Protococcus* has lost its capacity for all types of reproduction excepting cell division.

ORDER VII. OEDOGONIALES

General Characteristics. The order Oedogoniales, a small group, is important because its members have attained possibly the highest degree of heterogamy reached among the green algae. The filamentous plants, either branched or unbranched, characterize the group (Fig. 148). These plants grow in quiet water, usually attached to other plants, as upon the leaves and petioles of water lilies and similar aquatics. The outstanding characteristic feature in this order is a peculiar ciliation of the motile reproductive bodies. The numerous cilia of all the motile reproductive bodies, the zoospores, the androspores, and the male gametes, are attached in the form of a ring or "crown" at the anterior end of the structure. This feature separates the members of this order from those of all other orders of the green algae. The order is composed of three genera of which *Oedogonium*, a simple unbranched form, is the best known (Fig. 148). This genus is used as representative of the group.

Form, Structure, and Cell Differentiation. Considerable cell differentiation is found in both the branched and unbranched types. Usually the basal cell serves as a holdfast by the development of various outgrowths which attach the filament (Fig. 148, A). The sexual organs in all the genera arise by the modification of vegetative cells. These vegetative cells, which show a definite nucleus and cytoplasm, are characterized by the peculiar netted condition of the single parietal chloroplast, containing pyrenoids in varying numbers (Fig. 148, A, B). Cell differentiation is found in *Oedogonium*, since division is restricted to a portion of the filament. Increase in length of the filaments takes place by growth and division of certain cells. Often an individual cell undergoes several successive divisions, each leaving a characteristic cellulose "apical ring" or "apical cap." These, because of the repeated divisions of the protoplast, form a series of striations at the end of the cell.

Asexual Reproduction. Asexual reproduction in the genera of this group is by the formation of zoospores. As represented by *Oedogonium*, any vegetative cell may become a zoosporangium. In this event, the protoplast rounds up into a single zoospore which attains motility by means of the characteristic ring, or crown, of cilia at the anterior end. The zoospore escapes from the zoosporangium and swims away, retaining motility for only a short time. Soon it comes to rest upon a suitable substratum, loses its cilia, and grows into a new filament, the basal cell of which forms the organ of attachment, or holdfast, for the new plant.

Sexual Reproduction. One of the outstanding characteristics of the order Oedogoniales is the high specialization of the sex organs. Not only are the gametes highly differentiated into large nonmotile eggs and small motile sperms, but the sex organs, the oögonia and the antheridia, are often produced on separate plants. In the genus *Oedogonium* there are

three distinct conditions as regards the location of the sex organs, some of which result in considerable complication of the life histories of the plants. (1) The simplest condition, the monoecious, is that in which antheridia and oögonia are both produced in one bisexual filament. (2) A second condition is that in which the oögonia and antheridia are pro-

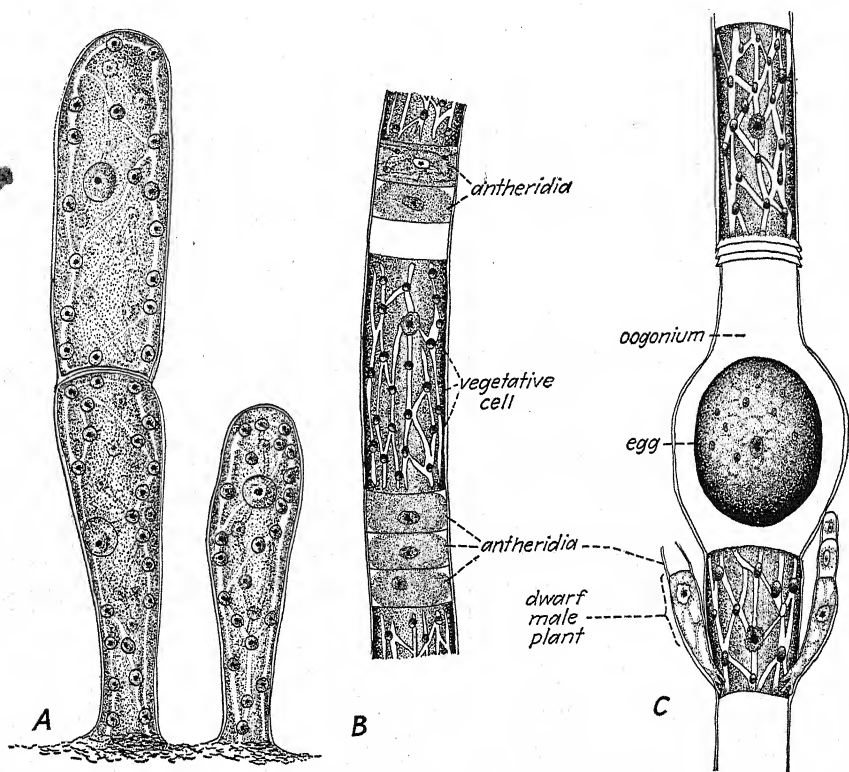


FIG. 148. *Oedogonium*. A, two young vegetative plants, one of a single cell, the other two cells, showing a single large nucleus and numerous pyrenoids on the net-like chloroplast; the basal cells in each case are holdfast cells; B, portion of filament showing cell content of vegetative cell and the formation of antheridia; C, portion of a filament showing oögonium, egg, vegetative cell, and two dwarf male plants, attached below the oögonium; the terminal cell of a dwarf male plant becomes an antheridium. (A, drawn by Helen D. Hill, B and C by Chris. Hildebrandt.)

duced in separate filaments, both of normal size; this is a dioecious condition, the filaments being unisexual. In both of these types of reproduction the antheridia are produced in a series by the repeated division of an ordinary vegetative cell. Each antheridium is a short cylindrical segment of the filament. An antheridium produces two motile sperms. (3) In the most complicated condition the oögonia are

produced upon ordinary female filaments, and the antheridia upon very minute filaments called the "dwarf male" plants (Fig. 148, *C*). This is also a dioecious condition. These dwarf male plants develop in a definite manner from a peculiar type of zoospore, called an **androspore**, which is smaller than the usual zoospore and apparently definitely associated with sexual reproduction. Androspores are produced in androsporangia, special sporangia formed by division from the ordinary vegetative cells. They are smaller than the regular zoosporangia and larger than the antheridia of the monoecious species, and the androspores are between the ordinary zoospores and gametes in size. They are provided with the characteristic crown of cilia and are motile when they escape from the androsporangia. They swim to the female filaments to which they attach themselves in the vicinity of the oögonia. The dwarf male plants develop from the androspores and consist of a few cells of which the terminal one becomes the antheridium. Each antheridium produces two small motile gametes, or sperms, which bear the crown of cilia characteristic of all the motile structures in this order.

The oögonia are highly differentiated structures, each one originating from a vegetative cell. The vegetative cell, by division, forms two cells, the basal one becoming the supporting cell of the oögonium, and the upper one the oögonium proper (Fig. 148, *C*). The protoplast of the oögonium becomes the female gamete, or egg, which, owing to the presence of chlorophyll, is green. Considerable food material, stored in the egg, is used in the development of the zygote after fertilization has occurred. The egg is nonmotile and remains permanently within the oögonium wall, which breaks at maturity near the region of a so-called "receptive spot." The motile sperm approaches the oögonium and is received in a bit of protoplasm which protrudes from the receptive spot through the break. The male gamete then penetrates the egg, and finally fertilization is effected when the nucleus of the sperm fuses with the nucleus of the egg. Thereupon the zygote develops a heavy wall and becomes a resting cell.

Germination of the Zygote. Through decay of the vegetative filament the zygote, or oöspore, is set free and undergoes a period of rest perhaps for a year or more. Meiosis precedes or accompanies germination of the $2N$ zygote into four $1N$ protoplasts that soon develop cilia and become capable of motility. Actual germination involves rupture of the zygote wall and liberation of the motile protoplasts, each of which may develop into a new vegetative plant.

Summary of the Oedogoniales. The Oedogoniales are separated from the order Ulotrichales, which they resemble, by the peculiar method of the attachment of the cilia of the motile reproductive structures. In

these structures the numerous cilia are arranged in the form of a ring, or crown, at the anterior portion of the motile structure. The members of the order have filamentous, septate, branched or unbranched plant bodies which generally grow attached to other aquatic plants. Asexual reproduction is by means of large zoospores produced singly in zoosporangia which develop from ordinary vegetative cells. Sexual reproduction is by a high-grade heterogamy in which the sex organs are highly specialized. Germination of the zygote is by very definite division into four protoplasts developing into zoospores which form the new plants.

ORDER VIII. SIPHONALES

General Characteristics. Although the Siphonales include a few fresh-water species, they reach their highest development in the warm salt waters of the subtropical latitudes. Many of them grow on the coasts of Florida, the West Indies, and similar latitudes on the Pacific Coast. The main feature of the group is the nonseptate and multinucleate nature of the plant body. This condition is termed **coenocytic**, and the plants are called **coenocytes**. These terms come from the Greek words *koinos*, meaning common, and *kytos*, meaning hollow, or as used in biology, cell. Thus coenocytes are plants having one common cell. In the true Siphonales, the only dividing cell walls, or septations, occur where organs of reproduction are formed.

All kinds and degrees of reproduction are found within the group. Some of the genera have asexual methods of reproduction, usually by means of zoospores, but no known method of sexual reproduction. In others, the reverse condition is found, sexual but not asexual methods being known, while, in still others, both asexual and sexual methods of reproduction may be well established. Sexual reproduction, where it is known in the various genera, varies from the simplest kind of isogamy to heterogamy in which there is an extremely high differentiation of gametes and gametangia.

Fresh-water Forms—Vaucheria. In the genus *Vaucheria* the plant body is an irregularly branched, filamentous structure with no septations or, in other words, is a single coenocyte (Fig. 149). The structure of the plant is that of a long tube with a thin wall, lined with a layer of cytoplasm in which are embedded numerous nuclei and many small disk-shaped chloroplasts. The central portion of the tube is occupied by a large vacuole. Cross walls occur only in the event of injury or in connection with the production of reproductive organs. The plants of *Vaucheria* grow in a tangled mass, the rather coarse branching filaments becoming interwoven into a loose thick felt. They grow both in water and on damp earth, sometimes covering several square feet of surface.

The asexual method of reproduction is by means of large motile zoospores which are formed singly in zoosporangia, cut off at the ends of the filaments by cross walls (Fig. 149, *B, C*). The contents of this terminal cell, or zoosporangium, consist of an oval mass of cytoplasm with numerous nuclei and chloroplasts. Two cilia are developed opposite each nucleus of the structure, and the whole body, when mature, escapes through an opening at the end of the sporangium. This coenocytic zoospore is intensely green in color owing to the presence of abundant chloroplasts embedded in the cytoplasmic layer. After a very short period of motility followed by a subsequent loss of the cilia, it forms a new plant by a simple process of germination.

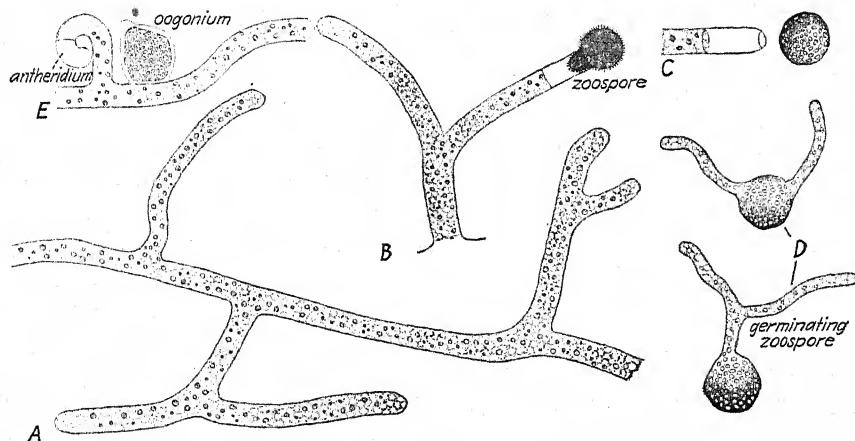


FIG. 149. *Vaucheria sessilis*. A, branching coenocytic filament; B-D, asexual reproduction; B and C, zoospore escaping from sporangium; D, zoospores germinating to form vegetative filament; E, sexual reproduction with antheridium and oogonium. (Drawn by Chris. Hildebrandt.)

In germinating, the zoospore elongates, often in two opposite directions, and by growth develops a new filament (Fig. 149, *D*). Germinating zoospores are easily recognized by the intensely green color and the appearance of a swollen portion of the filament representing the walls of the original zoospore. Multiplication by fragmentation may occur in *Vaucheria* as the result of injury.

The heterogamous sexual reproduction in *Vaucheria* is a rather complicated process. No other plant of the order Siphonales has attained the high degree of sexual differentiation seen in *Vaucheria*. The gametes differ greatly in size and are produced in distinct male and female gametangia, which are often borne on separate branches of the filament. There are some dioecious species within the genus, but most species are monoe-

cious. In monoecious species, the female sex organs, oögonia, and the male sex organs, antheridia, are generally produced on short branches close together on the filament. In some species, as in *Vaucheria geminata*, the sex organs are produced together on a short branch or stalk of the filament (Fig. 149, *E*). In most species, the oögonium is formed terminally on a very short branch or stalk, which is separated from the rest of the plant by a septum. In shape, the oögonium is spherical or ovoid with a short, rounded beak which opens to receive the sperm at the time of fertilization. At maturity, the contents of the oögonium consist of cytoplasm, a single rather large nucleus, numerous chloroplasts, and stored food in the form of oil. The contents of the oögonium form the large spherical female gamete or egg (also called the oösphere). The antheridium of *Vaucheria* is a slender, curled tubular structure separated by a septum from the short, slender branch upon which it is produced (Fig. 149, *E*). The contents of the antheridium consist of cytoplasm, numerous nuclei, and chloroplasts. At maturity, the numerous small male gametes or sperms are formed. Each sperm consists of a nucleus and a small amount of cytoplasm surrounded by a membrane. The sperms are laterally biciliate with the cilia attached far apart. The antheridia develop at the same time as the oögonia. When the oögonium is mature, the end of the beak opens slightly and a single microgamete enters. Actual fertilization, which may be delayed, consists of the fusion of the nuclei of the micro- and megagametes. Following fertilization, the zygote, filled with reserve food materials, develops a heavy wall and becomes a dark resting cell. After several weeks of rest, this heavy-walled cell, or zygote, germinates and directly forms a new *Vaucheria* filament. Cytological behavior at the reproductive stage has been insufficiently investigated, and evidence is conflicting. It is likely, however, that meiosis occurs in the zygote and is therefore like that in most filamentous green algae, zygotic meiosis. In such cases, the vegetative filaments are in the haploid condition and contain the 1*N* number of chromosomes.

Marine Forms. Owing to the occurrence of many genera of the Siphonales in the tropical oceans, it is impossible for the student in northern countries to form even an approximately adequate idea of the range of forms of the order by a study of the freshwater genera of the temperate zone. A few selected genera illustrative of the marine forms will, therefore, be very briefly discussed. The vegetative forms of the marine Siphonales are very diverse. They have assumed many unusual shapes and often the plant body is covered with a thick deposit of calcium carbonate.

One of the most striking types is that of the genus *Penicillus* (Fig. 150, *A*). It consists of a stalk portion composed of siphonaceous threads, the stalk expanding at the summit into a tuft of filaments. The whole plant is 3 or 4 in. in height and resembles a small inverted paint brush. The methods of reproduction are unknown. Another genus *Halimeda* has a remarkable vegetative form (Fig. 150, *B*). The plant body consists of a branched series of segments constricted at the base, the whole plant assuming

the form characteristic of the cactus *Opuntia* or "prickly pear." The only method of reproduction known is asexual by means of zoospores produced on small filaments growing from the margins of the segments. The genus *Codium* (Fig. 150, D) has a plant body composed of siphonaceous filaments interwoven to form a structure resembling a small rope of considerable length. Isogamous sexual reproduction occurs in the genus,

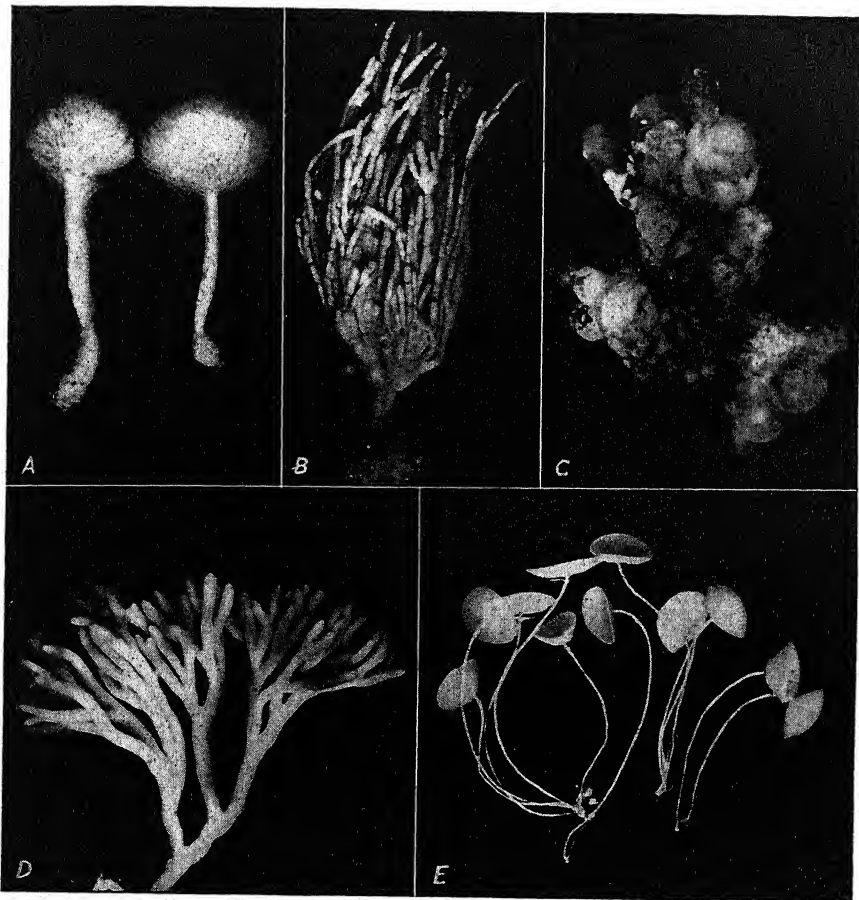


FIG. 150. Representative species of marine Siphonales. A, *Penicillus*; B, *Halimeda*; C, *Valonia*; D, *Codium*; E, *Acetabularia*.

the gametes being produced in gametangia borne terminally on the filaments. The gametangia occur on the periphery of the cord-like plant body. The plant body of the genus *Valonia* (in the order Siphonocladiales) consists of an irregular series of inflated lobed segments (Fig. 150, C). These forms are of very irregular size and shape and resemble small bottles. They frequently wash ashore and are commonly called "sea bottles." Reproduction is asexual by means of zoospores. A very striking form of plant body is that of the genus *Acetabularia* (Fig. 150, E) (order Siphonocladiales). These plants consist of a stalked portion with an expanded cap-like or disk-like portion

at the top. They resemble small slender mushrooms or toadstools (fungi). A rather complex isogamous sexual reproduction takes place in this genus, the reproductive bodies being produced in the disk-like portion.

Summary of the Siphonales. The prominent features, especially the coenocytic condition, indicates that the Siphonales are a side branch of the main line of algal development. Deposits of calcium carbonate, often seen in these plants, are, in general, unusual among algae. Although not universal, asexual reproduction by zoospores is common in the Siphonales, and both isogamous and heterogamous reproduction are found. Diversity in methods of reproduction is striking, and isogamy and heterogamy have little correlation with degree of structural development. Some genera appear to have the $1N$ number of chromosomes in the vegetative phase with zygotic meiosis typical. Others have $2N$ vegetative bodies with meiosis in the gametangia during maturation of gametes.

ORDER IX. CLADOPHORALES

General Characteristics. The Cladophorales are filamentous green algae, which may be either single or branched filaments composed of cylindrical cells placed end to end. The unique feature of this group is that the cells of the filament are coenocytic with numerous small nuclei and generally reticulate or disk-shaped chloroplasts.

Cladophora. Some species of *Cladophora* grow abundantly in the shallow water of lakes and streams; several are marine. The plants grow attached to rocks and structural timbers of various sorts, such as the piles supporting piers, submerged logs, and other substrata, and they may attain lengths of several inches. The plant body is a coarse, regularly branching, filamentous structure with numerous cross walls, separating the coenocytic segments (Fig. 151, A). The cell wall is rather thick and, as in *Vaucheria*, surrounds a parietal layer of cytoplasm in which are embedded the numerous rather large nuclei and the chloroplast, usually a netted structure with numerous small pyrenoids.

Asexual reproduction in *Cladophora* is accomplished by the production of numerous small uninucleate zoospores in the terminal segments of filaments (Fig. 151, B). The zoospores escape through an opening in the end of the sporangium, swim about for awhile, come to rest, and grow into a new plant. Besides the production of zoospores, asexual reproduction in *Cladophora* and related forms is accomplished through the formation of akinites in the cells of the filaments. In one genus of the order, *Pithophora*, the formation of akinites is the only known method of reproduction.

Cladophora has an isogamous method of sexual reproduction. Several hundreds of very small motile isogametes are produced in each game-

tangium, which is usually terminal like the zoosporangium. After escaping from the gametangium, the isogametes fuse in pairs. The zygotes usually germinate immediately, without undergoing meiosis, forming a $2N$ plant directly. Cytological investigations indicate that *Cladophora* has alternating plant forms with definite haploid and diploid chromosome numbers. The diploid plant developing from the $2N$ zygote produces zoosporangia. Zoospores result from the meiotic divisions occurring just before their formation. Haploid plants* developing from the $1N$ zoospores produce gametangia containing $1N$ isogametes. Fusions of these gametes to form $2N$ zygotes completes the life cycle.

Other well-known genera of the Cladophorales are *Rhizoclonium*, *Chaetomorpha*, and *Pilophora*.

SUMMARY OF THE CHLOROPHYCEAE, OR GREEN ALGAE

The characteristics of the green algae are (1) a well-organized, clearly defined type of cell structure with protoplast differentiated into definite nucleus, cytoplasm, and chloroplasts; (2) chloroplasts contain the green pigment chlorophyll and some yellow carotenoids; (3) photosynthetic products are sugars, with food reserves generally stored as starch, although some species, such as *Vaucheria*, accumulate oils; (4) vegetative forms ranging from single-celled plants, colonies, to multicellular plant bodies that may be filamentous or thallus types in the more advanced genera; (5) besides fragmentation, there are definite methods of non-sexual, or asexual, reproduction; (6) either isogamous or heterogamous sexual reproduction; (7) frequent though not universal zygotic meiosis.

Although showing considerable diversity of form, the green algae are simple plants with the filamentous type of plant body most common. In reproduction, they show the simplest conceivable methods, both asexual and sexual; they offer some indications of the method of origin of sexual reproduction in the similarity of production of gametes and zoospores in

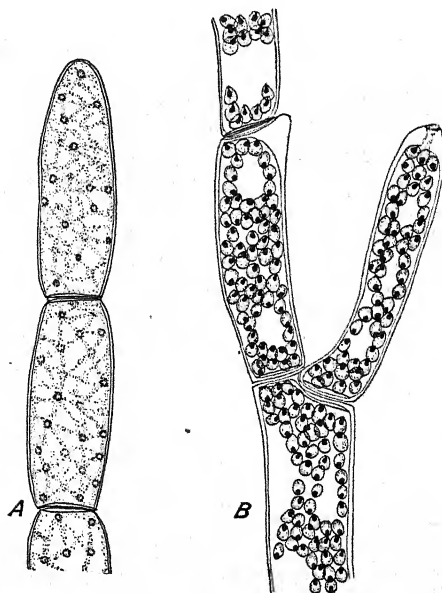


FIG. 151. *Cladophora*. A, terminal cells of a vegetative filament with numerous pyrenoids and nuclei; B, portion of filament showing numerous zoospores in each cell. (Drawings by Helen D. Hill.)

some of the isogamous genera like *Ulothrix*. It is generally thought that the chlamydomonad cell of the lower Volvocales represents the basic cell structure from which the higher green forms have been evolved. The topic of origins and evolution is one of great interest and significance in the Chlorophyceae.

With notable exceptions, as for example *Cladophora*, some of the marine Siphonales and *Ulva*, which may have diploid plant bodies, the vegetative structures of the green algae normally have the haploid or $1N$ number of chromosomes. The $1N$ condition, as may be illustrated by *Ulothrix* and *Oedogonium*, includes all modified cells, such as holdfasts, and the ordinary vegetative cells, all the asexual reproductive structures, such as zoospores, any nonmotile spores, and the gametes.

Syngamy, or fertilization, which is the union of the two haploid gametes, results in the formation of a single-celled diploid ($2N$) structure, the zygote. The zygote normally develops a thick wall and enters a period of "rest." Following this period of so-called rest, the zygote typically undergoes meiosis consisting of two nuclear divisions during which the chromosomes are reduced from the $2N$ back to the $1N$ number. As a result of the two meiotic divisions, four nuclei are formed each with the $1N$ chromosome number. A new cell is organized around each of these four nuclei. The four resulting cells are capable of growing into new vegetative plants. Because they resulted from meiosis, these cells may be called meiospores. The meiospores, which are frequently motile, may grow into new haploid alga plants. Generally, all four meiospores are functional as in *Oedogonium* and *Ulothrix*. In other algae, like *Spirogyra*, the desmids, and *Vaucheria*, two or three of them disintegrate, leaving the remainder to function.

Since meiosis occurs in the zygote of many algae, it is called zygotic, or initial, meiosis. In many green algae, the zygote is the only diploid structure produced in the life cycle. In some green algae, like *Cladophora* and in the higher plants generally, a well-defined diploid plant is generally produced from the zygote. In these diploid plants, meiosis is delayed until later stages in the life cycle. In contrast with zygotic meiosis, diploid plants are said to have intermediate meiosis.

As regards their classification, among the orders of the Chlorophyceae are the Volvocales, Chlorococcales, and Tetrasporales, all unicellular and colonial forms. The Ulotrichales, Chaetophorales, Oedogoniales, and Conjugales include many of the filamentous green algae. The Siphonales are coenocytic tubular algae with a variety of forms, mostly marine, and the Cladophorales are filamentous green algae with coenocytic cells.

THE CHROMOSOME CYCLE IN SEXUAL REPRODUCTION

In previous pages and in the pages that follow, mention is repeatedly made of meiosis and the behavior of chromosomes during sexual reproduction. Since a clear understanding of these matters is essential to a knowledge of sexual reproduction, particularly in the higher plant groups, they are briefly considered at this point.

Every organism arising by sexual reproduction develops from a $2N$ zygote which is the product of the union of a $1N$ male and a $1N$ female gamete originating in the male and female parental organisms. **Syngamy**, or **fertilization**, is thus the critical point in the life cycle at which the number of chromosomes is increased from the haploid to the diploid. As the zygote grows, the number of nuclei and cells is increased during the growth periods of the $2N$ generation through mitotic division (pages 201 to 209). The nucleus of each cell in the embryo, and in the adult developing from it, has the $2N$ number of chromosomes. When, however, such diploid plants produce spores, or animals produce gametes, the chromosomes are again reduced to the haploid number. This reduction in number is accomplished by two successive nuclear divisions called the **first and second meiotic divisions** (Fig. 152). Together they constitute the process of **meiosis** that occurs in the reproductive cells. The term *meiosis*, derived from the Greek word *meiōn*, meaning "less or reduction," is applicable because of the reduction in the number of chromosomes from the $2N$ to the $1N$ number that normally occurs during the process. In the two meiotic divisions there is a well-defined prophase, a metaphase, and an anaphase, in each of which a well-defined nuclear division spindle is evident, and finally a telophase with organization of the new nuclei. In these features the meiotic divisions resemble ordinary mitotic nuclear divisions occurring in growing tissues. *Meiosis differs from mitosis in its restriction to reproductive cells.* No mally it is not found, like mitosis, in ordinary body or somatic cells. Besides this distinction there are several other fundamental differences between the two processes.

The numerous species of plants and animals each have a characteristic number of chromosomes in the nuclei of the cells composing their bodies. The gametes of each species of plant and animal are likewise characterized by a definite number of chromosomes, which is normally exactly half of that in the nuclei of the body cells. The individual chromosomes differ in size, shape, and many minor structural features. These different types of chromosomes constitute a "set" or more technically a **genome** in each gamete. For each individual chromosome of the set in the male gamete there is a corresponding chromosome type in the female gamete. These two matching individual chromosomes are very much alike. They are similar not only in their external features but, in general, they carry equivalent or matching hereditary units, or genes. Union of the gametes, or syngamy, brings these types of chromosomes together in the zygote as pairs. Thus each parent, male and female, furnishes one member of every pair of chromosomes in an organism. Because of their origin and similarity in size, form, and general structural features, the two chromosome members are said to be **homologues**, which together constitute a pair of **homologous chromosomes**. For well-known organisms, these pairs of homologous chromosomes have been numbered. For example, in cultivated Indian corn, or maize, there are 10 chromosomes as the haploid, or $1N$ number, in each gamete and 10 pairs or 20 individual chromosomes as the diploid number in the zygote and other cells of the sporophyte. These chromosome pairs have been numbered according to their size with the largest designated as 1 and the smallest as 10.

In considering meiosis, it should be understood that regardless of their number, *all the pairs of homologous chromosomes are involved.* While in the following discussion de-

tails of the behavior of only one pair of homologues are given, all other pairs of homologous chromosomes are simultaneously undergoing the same process.

Meiosis. *The First Meiotic Division and the Separation of Homologues.* Cells capable of undergoing meiotic nuclear divisions, called **meiocytes** or **sporocytes**, are formed in the sporangia of plants and in the sex glands of animals where they may be designated as **oöcytes** and **spermatocytes**. Haploid, or $1N$, spores in all higher plants and gametes in animals are produced as a result of meiosis in the meiocytes. *Meiosis* is thus the critical point in the life cycle at which the number of chromosomes is reduced from the diploid to the haploid. One of the fundamental features of chromosome behavior during the prophase of the first division of meiosis, which differs from that found in mitosis, is the **pairing of the homologous chromosomes**.¹ In the process of pairing, the chromosomes appear to twist or coil around each other. Although actual fusion of these chromosomes does not occur during **synapsis**, as the process of pairing is called, the two homologues, or **synaptic mates**, of each pair do come into intimate contact throughout their length. While in contact, each member of the chromosome pair undergoes a longitudinal split forming two **chromatids**, or half chromosomes. Since it does not extend through the region of the spindle fiber attachment, or **centromere**, the longitudinal split in the original chromosome is not absolutely complete. The chromatids thus held together in the region of the centromere form chromatid pairs and together represent the original chromosome. Because the two members of the pair of homologous chromosomes are in contact at the time of the longitudinal splitting, there are actually two pairs of chromatids forming a four-partite structure, the **chromosome tetrad** or perhaps more properly, the **chromatid tetrad**. Although each chromosome is now composed of two chromatids, while they remain attached in the region of the centromere, this bipartite structure may still be considered as a single chromosome. As the prophase of the first meiotic division draws to a close, the chromosome tetrads move toward the equator of the division spindle. During the metaphase of the first division, the chromosome tetrads are located at the equatorial region of the spindle forming the equatorial plate.

The Anaphase and Reduction in Chromosome Numbers. During the anaphase of the first meiotic division, the original chromosome members of each pair of homologous chromosomes are separated and, with their two chromatids still held together at the centromere, move to opposite poles of the division spindle and eventually into different nuclei (Fig. 152). In this way, the four chromatids of the chromosome tetrad are separated into pairs, which may now be called **chromosome diads**, or **chromatid diads**. Since the two chromatid members of each diad pair actually constitute an original chromosome, their separation during the anaphase of the first division results in the separation or disjunction of the two members of the original pair of homologous chromosomes. Each **secondary meiocyte**, formed as a result of the first meiotic division, receives one chromosome diad, representing one of the members of each original pair of homologous chromosomes. Thus the $2N$ number of chromosomes found in the primary meiocyte is reduced to the $1N$ number in each of the secondary meiocytes. During the telophase of the first meiotic division, the chromosome pairs are rounded up into the nuclei of the secondary meiocytes. Accompanying the division of the nucleus, **cytokinesis** generally, but not always, occurs, and two secondary meiocytes are formed from the

¹ In order that the relations of the meiotic processes to chromosome numbers may be briefly considered, reference to exchange of pieces between chromatids, chiasmata, and the relationship of these to crossing over are purposely omitted in this discussion.

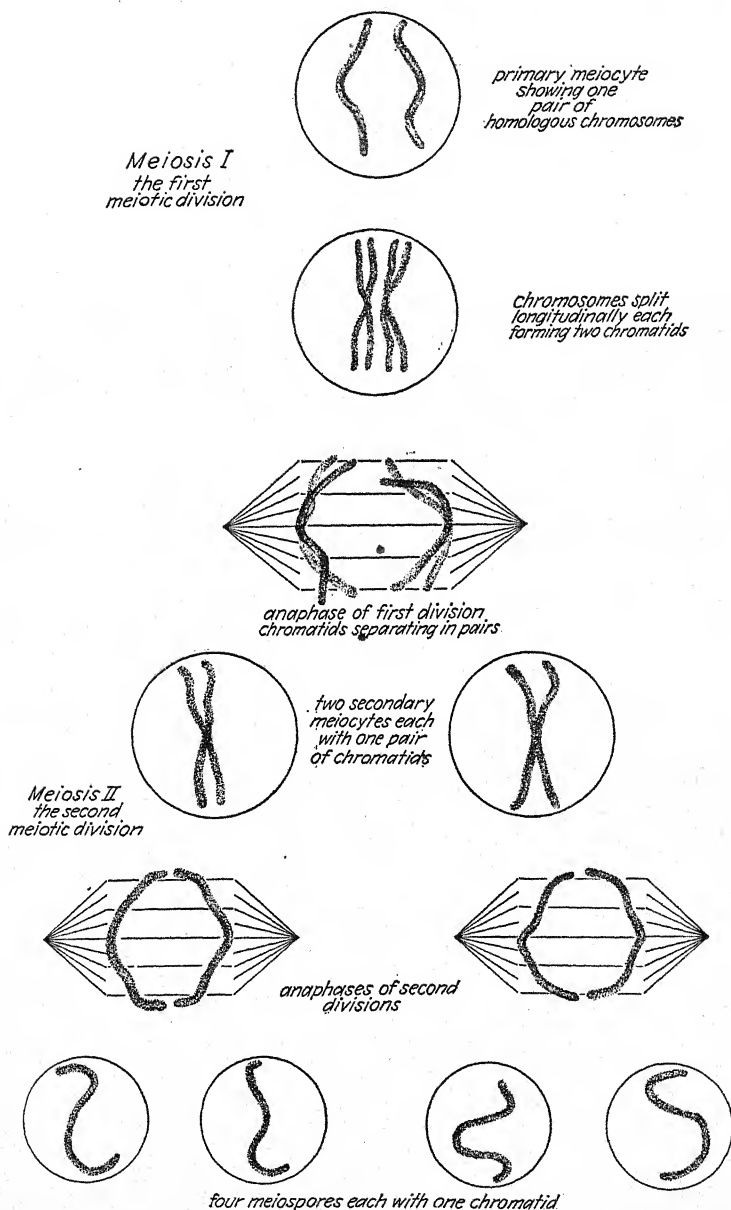


FIG. 152. Meiosis. Diagrammatic scheme illustrating chromosome behavior during the first and second meiotic divisions. Explanation in the text.

original primary meiocyte. Secondary meiocytes in plants may or may not be separated by cell walls.

The Second Meiotic Division and the Separation of Chromatids. In plants, a second meiotic division with prophase, metaphase, anaphase, and telophase occurs in each of the secondary meiocytes, or **secondary sporocytes**, as they are often called. An important feature distinguishes the second meiotic division from the first. Since there is only one member of each original pair of homologous chromosomes present in the secondary meiocytes, there is no pairing of chromosomes in the second division. Because the members of each original pair of homologous chromosomes are already longitudinally split into two chromatids, there is no further splitting of the chromatids during the second meiotic division. During this second meiotic division, the centromere, holding the chromatids of each chromosome diad, is divided. The chromatids of each pair thus released are separated, each passing intact to one of the poles of the division spindle and eventually into a different nucleus (Fig. 152). This behavior separates the four chromatid members of the original chromosome tetrad and distributes one of them to each of the four meiospore nuclei that result from meiosis. In this way, the number of chromatids is reduced to the $1N$, or haploid, number in each meiospore. Comparisons of mitosis and meiosis should emphasize that *in mitosis a longitudinal splitting of every chromosome into two chromatids is followed by a single division of the nucleus. For this reason, there is no change in chromosome numbers during ordinary somatic mitosis. In meiosis there is a longitudinal splitting of all chromosomes, each forming two chromatids. This single splitting of the chromosomes, however, is followed by two complete nuclear divisions.* This fundamental feature is responsible for the reduction in chromosome numbers which regularly accompanies meiosis. In fact, two meiotic nuclear divisions are necessary in order that a reduction in the number of chromatids to the haploid may be accomplished. The meiotic divisions are important not only in reducing the number of chromosomes from the diploid to the haploid number, but also as cellular mechanisms for the segregation and assortment of the contained hereditary units or genes. An understanding of meiosis is fundamental in studies of heredity.

During the telophase of the second meiotic division, the four chromatid groups, each numbering 10 in the corn plant, are rounded up to become the haploid chromosome set in the nuclei of the four meiospores formed from each of the original meiocytes. The four meiospores are frequently referred to as a "quartet" of spores. The appearance of the quartet of spores varies in different kinds of plants. In some cases, the spores may be arranged in a row or in linear arrangement; in others, they are tetrahedral and arranged in a spherical mass often surrounded by the wall of the original meiocyte. When spores formed as a result of meiosis germinate, they grow into gametophytes of varying degrees of complexity. Increase in the number of nuclei and cells occurring during the growth and development of the $1N$ gametophyte takes place by ordinary mitosis, as it does in the somatic, or body, tissue of the $2N$, or sporophytic, generation.

Comparison of Fertilization and Meiosis. *Fertilization and meiosis are compensating processes in reproduction that serve to keep the chromosome numbers in a state of equilibrium from generation to generation. Union of haploid gametes brings the number of chromosomes in the zygote up to the diploid number. Then, at the time in the life cycle when meiosis occurs in the meiocytes, the chromosomes are again reduced to the haploid number. Relationship of fertilization and meiosis in point of time also varies in different organisms. In animals, union of gametes, or fertilization, results in the formation of the zygote. Development of the embryo follows, and*

eventually when the animal is mature, meiosis occurs in the sex glands, or gonads, forming gametes immediately. Meiosis of this type is called **gametic**, or **terminal**, **meiosis**. In some of the lower plants, such as certain genera of the green algae, fertilization forming the zygote is followed by meiosis in this zygotic cell at an early date. This type of meiosis is called **zygotic** or **initial meiosis** (Fig. 142). In most of the plants higher than the algae, meiosis occurs in meiocytes formed within sporangia. Because in these cases meiosis occurs late in the life cycle, at some time after fertilization, and the meiotic products are $1N$ spores which may grow and develop into haploid gametophytes, **meiosis** in these plants is designated as **sporic**, or **intermediate**, in contrast with the other two types.

Comparison of Mitosis and Meiosis. The processes of mitosis and meiosis are similar in that each has the characteristic prophase, metaphase, and anaphase, with nuclear division spindles, and a final stage, or telophase, during which new nuclei are organized. Mitosis and meiosis differ, however, in several details. Mitosis occurs in all meristematic or growing tissues, both somatic and reproductive, while meiosis is normally restricted to the final two divisions of the nuclei in the reproductive tissues, in the sporangia of plants and in the ovaries and testes of animals. Further differences between the two processes are found in the behavior of the members of the pairs of homologous chromosomes. During mitosis, not only in haploid, or $1N$, cells, but also in diploid, or $2N$, cells where both members of each pair of homologous chromosomes are present, *the individual chromosomes act independently*. Each chromosome splits longitudinally, forming two chromatids that separate and pass into new nuclei during the nuclear division. *No pairing of homologous chromosomes occurs in mitosis*. Successive nuclear divisions are independent. *In mitosis, characteristically a single nuclear division follows each longitudinal splitting* (Figs. 90, 91). This type of nuclear division may continue through many cell generations *without change in chromosome number*.

During normal meiosis, which occurs only in diploid (or in polyploid) tissue, *the members of the pairs of homologous chromosomes act together, pairing previous to the nuclear divisions*. This pairing is accompanied by a single longitudinal splitting of each individual chromosome and results in the formation of a *group of four chromatids*, the **chromosome tetrad**. This one longitudinal splitting of the chromosomes, characteristic of the prophase of the first meiotic division, is all that occurs; there is no further splitting of chromosomes in the whole process. This event, however, *is followed by two complete nuclear divisions*, the first and second meiotic divisions, in which the chromosome behavior in the second division is definitely dependent on the characteristics of the first. It is this particular relationship of one longitudinal splitting of chromosomes followed by two complete nuclear divisions which makes possible a reduction in chromosome numbers (Figs. 152, 297, 299, 304, 305).

THE CHARALES

The Charales, represented by the well-known genera *Chara* and *Nitella*, constitute a group of green plants that have uncertain affinities with other plant groups. They grow submerged, attached by rhizoids to the mud, forming thick masses at the bottoms of small pools and slowly flowing streams. The plant body is slender and flexuous with individual plants attaining lengths of 6 to 12 in. The multicellular plant has a whorl of short branches at each node (Fig. 153, A). Internodes consist of a single elongated cell, but several short cells enter into the structure of the nodes.

The short branches also have nodes and internodes such as are characteristic of the main axis. In some genera, but not all, the internodal cells become overgrown by sheath cells arising from basal nodes of the whorl of branches. In cross section, an ensheathed internode shows the central internodal cell as the main axis, surrounded by smaller sheath cells.

Incrustations of calcium carbonate typically found in some genera such as *Chara* are reflected in their common name *stonewort*. Other genera like *Nitella* are free of such deposits. Cells of the Charales are multinucleate

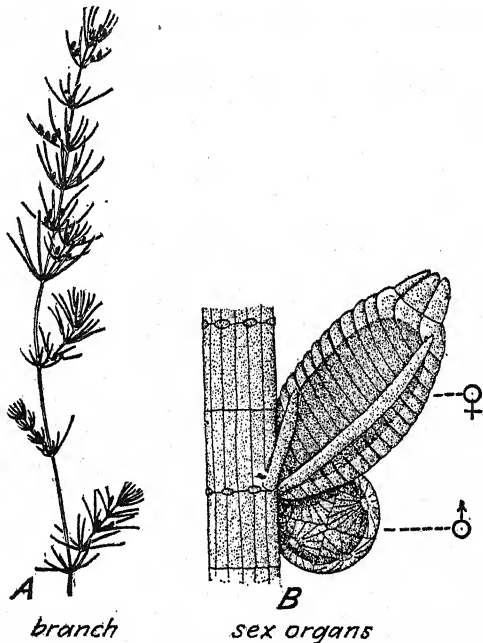


FIG. 153. *Chara*. (From Gilbert M. Smith, "Cryptogamic Botany," Vol. I. By permission of the author and courtesy of McGraw-Hill Book Company Inc., New York.)

with numerous small chloroplasts embedded in a fixed layer of peripheral cytoplasm. An inner layer exhibits very conspicuously a rotary streaming movement.

Reproduction. The only known method of asexual reproduction in the Charales involves detachment of various vegetative outgrowths which develop into new plants. Sexual reproduction is heterogamous. The organs of reproduction in the Charales are complex multicellular structures markedly different from the simple one-celled sex organs generally characteristic of the Thallophyta. The sex organs are borne near the nodes of the main axis in a position axillary to the short branches (Fig. 153, B).

They originate from the nodal cells at the base of a branch with the female structure above the male. In some species, however, male and female sex organs are produced on separate plants. The male sex organ is spherical, multicellular, and of a bright orange color at maturity. Coiled, biciliate sperms are formed one in each cell of long filaments inside the male sex organ. These internal structures probably are homologous with single-celled antheridia of the filamentous green algae. The female sex organ, green in color, is ovoid and covered by several spirally twisted filaments that are united above, forming a pointed apex. The female gamete is the uninucleate protoplast of the central cell of the organ. The sperms reach the eggs by passing between the apical cells of the sheathing filaments of the female sex organ. Following fertilization, zygotic meiosis results in four meiospore nuclei. Three of these disintegrate leaving one that functions as the nucleus of a nonmotile spore. This spore germinates and reproduces the plant.

CLASS BACILLARIOPHYCEAE

The Bacillariophyceae, commonly known as the diatoms, are single-celled microscopic algae of diverse forms, which are variously colored but generally yellow or brown. Some of them exhibit slight motility. They occur in both fresh and salt water and in damp soil and though widely distributed appear to thrive best at cold temperatures. The diatoms form an important part of plankton, the basic food of aquatic fauna. The preservation of the remains of diatoms as fossils in vast deposits of "diatomaceous earth" is an indication of their abundance in and persistence through past geological ages. Smith estimates that there are about 170 genera and more than 5,000 species of diatoms, both fossil and living. Two large groups are recognized, the orders Centrales and Pennales. The members of the Centrales occur as round, generally nonmotile forms (Fig. 154, A). In this order, the markings on the walls present a radiate appearance. In the Pennales, the elongated organisms are boat- or needle-shaped with markings appearing pinnately (Fig. 154, B). Motility is common among the Pennales.

The Nature of the Cell Wall. An outstanding feature of diatoms is the nature and structure of the cell wall, which consists of two overlapping parts or valves, one slightly larger than the other, which are described as "fitting together like the two parts of a pillbox." This structural characteristic is the basis for the name diatom, which means "cut in two." Because of the structure of the wall, diatoms present two views to the observer, from the top or bottom the valve view and from the sides where the parts of the box-like wall overlap, the girdle view.

Chemically, the wall of a diatom is composed of the organic substance pectin and the inorganic compound *silica*. Opinions differ as to the dis-

position of these two substances. Some investigators think of the wall as consisting of an outer silicated structure and an inner layer of pectin. Others regard the wall as composed of pectin impregnated with silica. If viewed under the proper magnification, conspicuous striations on the walls of diatoms appear to be composed of dots. Among the Centrales the dots are usually large and arranged radiately. In the Pennales, where the dots may be extremely small, they can be seen only with high magnification. Arrangement in this group is pinnate, the dots appearing in

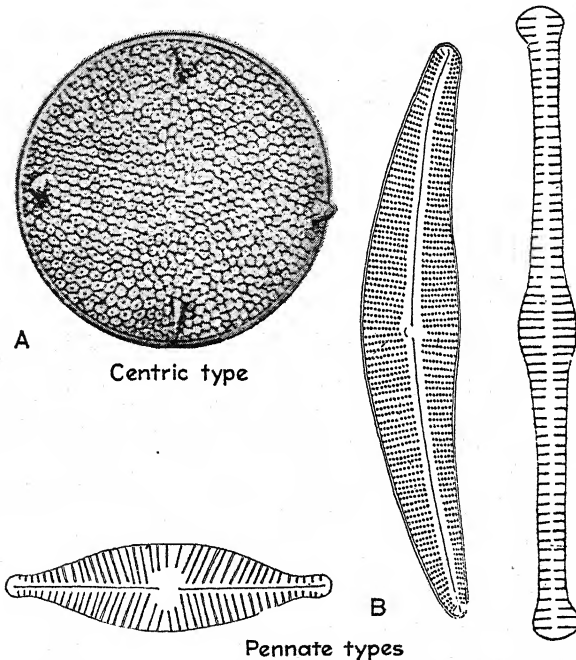


FIG. 154. Types of diatoms. (From Gilbert M. Smith, "Cryptogamic Botany," Vol. I. By permission of the author and courtesy of McGraw-Hill Book Company, Inc., New York.)

regular rows near the edges of the valves and extending inward to near the middle. Individually the larger dots are thought to be thin places in the walls while in some cases the smaller ones appear to be pores.

On the back of each valve of most of the elongated types, there is an additional marking called the **raphe**. The word means "seam" or "stitch." Structurally the raphe is a V-shaped slit or cleft in the wall which extends from end to end of the valve and which is V-shaped in cross section. **Nodules**, which are also structural modifications of the cell wall, terminate the raphe and interrupt it near the mid-point. Markings on the wall of

diatoms, striations, raphe, and nodules constitute taxonomic criteria. Part of the distinguishing features of the orders, families, and genera consist of the presence or absence of raphes, the nature of the nodules and the size and distribution of the dots constituting the striations on the walls of the valves.

The Structure of the Protoplast. The protoplast of a diatom consists of cytoplasm closely appressed to the cell wall and generally a large central vacuole. In species with elongated cells, the vacuole is frequently bridged at the middle by a large strand or band of cytoplasm which carries the relatively large nucleus. Depending upon the species, the cell may contain a single large plastid, a few medium-sized, or several small ones. The chlorophyll they contain is often masked by the presence of additional yellow or brown pigment designated as diatomin. Oil is a stored food product and the gelatinous, or mucilaginous, material covering the cell is thought to be pectic acid.

Motility of Diatoms. Members of the order Centrales apparently are nonmotile, motility being restricted to the Pennales. Many but not all of the pennate types are motile, with movements slow and jerky and confined to forward and backward directions. Cause of movements in diatoms has been a topic of considerable speculation. The best explanation of their movements appears to be one associated with the flow of currents of water set up by the circulation of cytoplasm in the protoplasm.

Methods of Multiplication. Diatoms multiply by a peculiar method of cell division. As the cell increases slightly in diameter, the valves separate. The nucleus undergoes mitosis with the division spindle parallel to the short axis of the cell in a manner that ensures longitudinal division of the protoplast. If there is a single plastid or several large plastids, each one of them undergoes division, a half passing eventually into each daughter protoplast. When there are numerous small plastids, some of them pass into each of the daughter protoplasts and there divide to restore the original number.

Division of the nucleus is followed by division of the protoplast along the median line of the longitudinal axis. Thus two protoplasts are formed from the original one. When division has been completed, each cell has one siliceous valve, but the side along the plane of cell division is bounded only by a protoplasmic membrane. The peculiarity of the process is found in the manner of new wall or valve formation. Each daughter protoplast grows a new valve to match the one remaining from the original cell wall. In each case, this new valve fits inside the original with the result that one new diatom is the same size as the parent and one is slightly smaller. Cell division is reported as taking place at night, and it is said to be fairly rapid. Because of frequent multiplication and the tendency

for some of the cells to be reduced in size, part of the diatomaceous population soon becomes more diminutive.

Auxospore Formation and Rejuvenescence. When the small diatom cells reach a size incompatible with physiological processes, auxospores are formed and restoration of normal size and physiological rejuvenescence follow. The prefix *auxo-* in the term auxospore comes from the Greek and means "grow." An auxospore then is a growth spore, or an enlarged spore, and refers to the increased size of the auxospore as compared with the diminutive vegetative cell or cells giving rise to it.

Auxospores are apparently formed in two distinct ways. One type is strictly nonsexual and appears to be merely an enlargement of the vegetative cell. The other type is preceded by meiosis and gamete formation with cell fusion. It appears to be an authentic sexual process. In the nonsexual process, the valves of the diminutive cell separate and the released protoplast enlarges to several times its former size. When normal size for the species has been restored, two new siliceous valves are formed around the protoplast. Auxospore formation by sexual processes is accomplished in several different ways, with considerable variation in nuclear behavior. It appears that in general, perhaps always, the vegetative diatom is a diploid structure. Therefore, if the nucleus of such a diatom undergoes the two meiotic divisions, haploid, or $1N$, nuclei would be formed. Variation in cytological details occur in the different genera of diatoms, but it may be assumed that meiosis with a reduction of chromosome numbers generally takes place. The haploid cells thus formed escape from the valves and fuse. The resulting cell grows into an enlarged protoplast that develops into the auxospore or renewal spore. Normal vegetative cells are formed from the auxospore.

THE PHAEOPHYCEAE—BROWN ALGAE

GENERAL CHARACTERISTICS

The Phaeophyceae, or brown algae, are a widely distributed group of marine forms that attain their greatest development in the colder waters of continental coasts in the north temperate zone. Their color, varying from dark brown to olive green, results from a brown carotenoid pigment, fucoxanthol. This pigment, a characteristic of the group, is located in the plastids, where it tends to obscure the green chlorophyll. The brown algae show great diversity in form and structure. For example, *Ectocarpus* is a small filamentous plant, while *Laminaria*, *Macrocystis*, and *Nereocystis* are massive seaweeds called the giant kelps. Although some species of kelps are relatively small plants, only 3 or 4 ft. in length, many are giant forms and reach lengths of 300 ft. or more comparable to the heights of tall forest trees. The weight of these giant algae when dried, however,

amounts to only a few pounds. Besides a holdfast, the kelps have a long, slender flexuous stalk and an expanded blade that may be entire or dissected (Fig. 155). The blade portion grows from the activity of a group of meristematic cells located at its base. This growing region may also renew blades frayed by wave action.

Another group of brown algae known as the "rockweeds" is commonly found along the rocky coasts of the temperate zones. The species of *Fucus* (Fig. 156, A) are the best known of this group of the brown algae. The genus *Ascophyllum*, closely related to *Fucus*, grows in similar habitats. These plants grow attached to rocks at the shore line where the plants are often alternately exposed and submerged owing to the ebb and flow of the tides. *Sargassum*, the "gulfweed" (Fig. 156, B), grows either attached to rocks or free floating. *Sargassum* makes up a large part of the conspicuous vegetation of the Sargasso Sea, a great ocean eddy in the southern part of the North Atlantic Ocean. The plants in this group represented by *Fucus*, *Ascophyllum*, and *Sargassum* are of medium size, ranging from a few inches to 1 or 2 ft. in length. In general form, the plant body is a ribbon-like thallus, with holdfasts and air bladders.

Generally, brown algae grow attached by holdfasts to rocks near the ocean shore line where at least at high tide they may be submerged. Some kinds, like *Fucus* and *Sargassum*, may live for some time as free floating plants. Many of the smaller filamentous ones like *Ectocarpus* grow as epiphytes on the larger seaweeds.

The kelps and rockweeds are of limited economic importance. Commercial iodine and potash once extracted from some brown algae can now be more economically obtained from accessible mineral supplies. Brown algae are used as fertilizer for gardens and agricultural land along the coastal areas of certain European and Asiatic countries. They also constitute an item of diet for some Oriental peoples.



FIG. 155. A species of *Laminaria*, one of the kelps, showing the well-developed, branched holdfast, the short stem, and the well-developed blade.

Cell differentiation is more pronounced in the kelps than in the thalli of any other algae. In the stalks differentiation of cells makes an epidermal layer, cortical and central regions recognizable. Besides these, connecting filaments that often extend in radial direction and an elaborate system of mucilage canals are developed in the stalks. Some conducting cells have the structure and appearance of the sieve tubes of the higher flowering plants, with protoplasmic strands passing through the openings of the sieve plates. These tissue differentiations are continued into the blades of the kelps, though less markedly (Fig. 160).

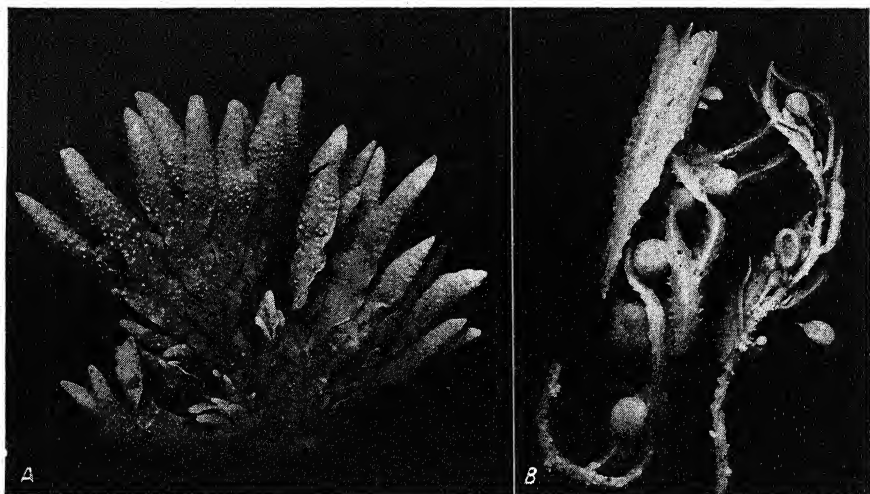


FIG. 156. *A*, a species of *Fucus*, showing the fruiting tips or receptacles, which contain the conceptacles that open to the exterior through the white raised pores. Note the dichotomous branching of the thallus. *B*, a species of *Sargassum*, showing the stem-like and leaf-like parts, as well as the rounded swollen bladders, or floats.

Cells of the brown algae have definite nuclei, cytoplasm, and chloroplasts. The chloroplasts contain, in addition to the green chlorophyll pigments, yellow xanthophyll that is probably in excess of the green. A brown carotenoid pigment, fucoxanthol, also present in the chloroplasts masks the green chlorophyll and produces the characteristic brown color of the Phaeophyceae. The products of photosynthesis in the brown algae are sugars. Food reserves are stored as simple sugars, the alcohol manitol and complex polysaccharides such as laminarin. This is in contrast with the green algae where carbohydrate food reserve is generally starch. In the brown algae, the motile reproductive cells, zoospores and gametes, have two cilia of unequal length, which, generally, are attached laterally.

Nine orders are recognized in the brown algae. Of these groups, repre-

sentative genera of four, the Ectocarpales, the Laminariales, the Cutleriales, and the Fucales are discussed in the following pages.

LIFE HISTORIES OF REPRESENTATIVE GENERA

Ectocarpus. The genus *Ectocarpus* is one of the best known of the lower brown algae. The plant body is composed of small branched filaments, which grow in tufts attached to the larger marine algae and other suitable substrata. These filaments may be a single strand of cells or they may consist of several rows of cells joined together. In structure the plant is not more complex than many of the green algae. Each of the cells of the filament contains a protoplast consisting of a nucleus, cytoplasm, and chloroplasts. The chloroplasts are plate-like in form, sometimes slit or split in such a manner as to give the appearance of a network.

In *Ectocarpus*, as well as in the other related lower brown algae, there are two types of reproduction, asexual and sexual. Asexual reproduction occurs through the production of zoospores which germinate directly to produce new plants. Sexual reproduction is accomplished by the fusion of two anisogametes, forming a zygote that develops into a new plant.

Among many investigations of the life cycles of *Ectocarpus* and related genera that of Papenfuss, published in 1935, is notable. *Ectocarpus siliculosus*, the species perhaps most extensively studied, has two kinds of plants; one is the sporophyte with the diploid number of 16 chromosomes, and the other is the gametophyte with the haploid number of 8 chromosomes. With the exception of the smaller size of the haploid plants, their plant parts and cells, the sporophytes and gametophytes are essentially alike in appearance. The diploid plant produces two kinds of reproductive organs, one a compound multicellular structure, the plurilocular sporangium, and the other, a single-celled structure, the unilocular sporangium. The plurilocular sporangium is elongated, circular in cross section, and, as its name indicates, contains many cubical compartments (Fig. 157, B). Usually a single motile zoospore, or gonidium, is produced in each of these one-celled compartments. Since this development occurs without change in chromosome number, each zoospore has the diploid number of 16 chromosomes. At maturity, the zoospores escape from the plurilocular sporangia, and if they reach a favorable location, may germinate and produce a new diploid plant similar in every way to the parent plant. These plurilocular sporangia, with their diploid zoospores, thus furnish a means of rapid asexual multiplication of the sporophytic plants.

At certain seasons of the year, the same or different diploid plants produce the single-celled unilocular sporangia. The single diploid nucleus of the young sporangium, with 16 chromosomes, undergoes meiosis and

reduction in chromosome number, producing four meiospores, each with the haploid number of 8 chromosomes. These meiospores while still within the unilocular sporangium undergo three (or sometimes four) mitotic divisions, each one normally producing 8 (or sometimes 16) haploid cells that represent early stages of the gametophytic phase in the life cycle. Each of the haploid cells formed in this way rounds up and develops a reproductive body which escapes from the sporangium as a motile cell

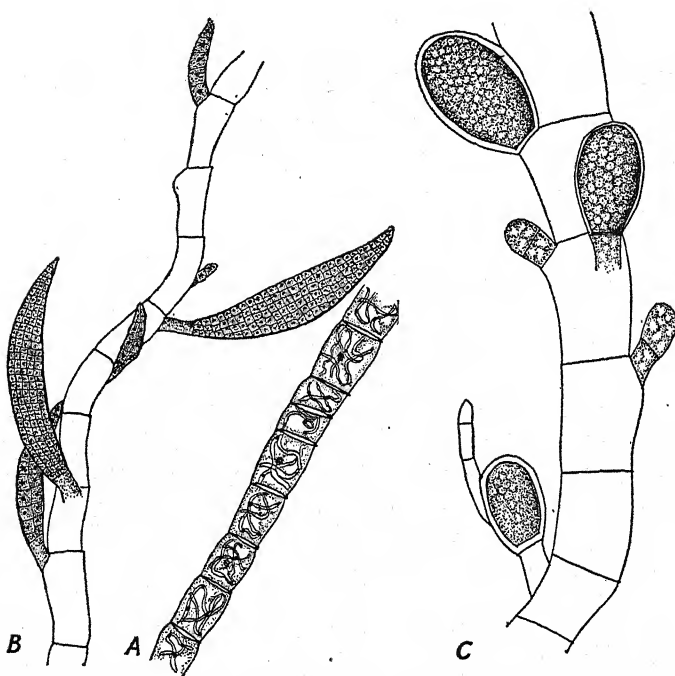


FIG. 157. *Ectocarpus*. A, small portion of a vegetative filament; B, plurilocular gametangia on a filament; C, unilocular sporangia on a filament. (Drawings by Helen D. Hill.)

or zoospore. Under suitable environmental conditions, the zoospores may grow into the alternate gametophytic type of plants which, like the zoospores, have 8 chromosomes. They develop only compound reproductive structures similar to the plurilocular sporangia of the diploid plants, except that they are smaller. Each compartment of the plurilocular sporangium produces a single motile reproductive cell that normally fuses with another one of similar size to form a zygote. Since these reproductive cells are capable of taking part in fertilization, they are true gametes, and the plurilocular structures developed on the haploid plants are in fact gametangia. Although the fusing gametes are of the same size and are

morphologically alike, they are physiologically unlike. It has been shown that gametes from the same plant never fuse with each other. Fusion does not always occur between the gametes from any two different plants, but only between those from certain different plants. This behavior indicates that the haploid generation of *Ectocarpus* actually consists of two kinds of genetically and therefore physiologically different plants which are however morphologically alike. They are really dioecious plants that produce distinctly male and female gametes. Such similarly sized but physiologically different gametes may be considered physiologically as **anisogametes** and the sexual condition as physiological **anisogamy**.

Papenfuss observed that fusion of gametes in fertilization occurred only between a female gamete that had ceased to swim and was attached to the substratum and a single motile male gamete. Fusion of the 8- chromosome gametes leads to the formation of a 16-chromosome zygote. When these diploid zygotes germinate, they grow into diploid plants. Thus the sexual life cycle from diploid plants, through haploid zoospores, haploid plants that produce gametes, and finally $2N$ -zygotes is completed with the development of the new sporophytic plants.

Numerous observations seem to confirm the suggestion that occasionally gametes produced in the plurilocular gametangia on haploid plants of *Ectocarpus* may grow directly into new plants without fertilization. This behavior, called **parthenogenesis**, is the growth of a gamete into a new plant without the physiological and genetic stimulus of fertilization. The new plants developed in this manner are haploid structures with 8 chromosomes. It has been suggested that only the physiologically female gametes are capable of parthenogenetic development. Parthenogenesis thus provides a means of asexual multiplication for the haploid or gametophytic generation.

Some investigators of the life cycle of *Ectocarpus* have reported the fusion of haploid zoospores from the unilocular sporangia of sporophytic plants. In these cases, it was suggested that fusions occurred in groups with numerous motile cells, possibly functioning as males, collected about and attempting to fuse with a single motile cell, possibly functioning as a female gamete. But in no case of this kind was the development of a zygote observed. The accuracy of this observation and the suggestion of the fusion of zoospores have been questioned. From observation of true fertilization, where a single motile male gamete fused with a female that had "come to rest" on a suitable substratum, Papenfuss concluded that zoospores clinging together as they escaped from the sporangium had been mistaken for fusion of these structures. According to Papenfuss, meiosis and the reduction of chromosomes occur only in the unilocular sporangia borne on diploid plants. Furthermore, true fertilization probably occurs at one stage in the life cycle and only when true gametes, with the haploid number of 8 chromosomes, fuse to form the zygote with 16 chromosomes.

An interesting observation is that many of the marine algae are obligate epiphytes, *i.e.*, they can grow and develop only when they are attached to other living plants

belonging to certain genera and species. In some localities of the Woods Hole area of the Atlantic Coast, it was found that while the diploid plants of *Ectocarpus siliculosus* grow attached to *Chorda* and a few other brown algae, the haploid plants are found only when they can grow attached to *Chordaria*, still another of the brown algae. Plants restricted in this way are called **obligate epiphytes**. This epiphytic relationship, therefore, restricts the 1N plants or gametophytic phase to those regions and localities where *Chordaria* grows. This fact may explain the failure of certain investigators to find the haploid plants of *Ectocarpus* and the inconsistencies in some of the published accounts of the life history of *Ectocarpus*. *Pylaiella*, a genus related to *Ectocarpus*, has a similar epiphytic relationship. In this genus, diploid plants grow attached to both *Fucus* and *Ascophyllum* of the brown algae. The haploid plants of *Pylaiella* are, however, confined as obligate epiphytes on *Sertularia*, itself epiphytic on *Ascophyllum*.

Fucus and Related Genera. The plant body of *Fucus* consists of a flat, dichotomously branched thallus of an olive green or brownish color. The macroscopic plants normally grow firmly attached by an expanded holdfast to completely or partly submerged rocks. When covered, the thallus is buoyed up in the water by bladder-like structures, or floats. The habitat of the rockweed is between high and low tide water on rocky coasts of the temperate oceans. In this location the alternate submergence and exposure are important features related to the release of gametes.

The only known method of **asexual reproduction** in *Fucus* is by fragmentation. When this occurs, broken pieces may continue to live as floating plants. This is found especially in the related genus *Sargassum*. **Sexual reproduction** is heterogamous. Small actively motile microgametes or sperms fertilize very much larger nonmotile macrogametes or eggs.

The plant body of *Fucus* is diploid with 64 chromosomes in at least one species. Before the significance of the chromosome cycle was recognized, the reproductive structures of *Fucus* were thought to be the sex organs, antheridia and oogonia. These names are still retained in some discussions. Investigations show, however, that meiosis takes place and that meiospores are actually produced in the reproductive structures, which may therefore be called sporangia. The *Fucus* plants are then sporophytes, *i.e.*, spore-producing plants. Since the spores and their final products are of two different sizes, the terms microsporangia and megasporangia may be properly applied to them. These sporangia together with sterile filaments, called **paraphyses**, are produced in small cavities known as **conceptacles**, which are aggregated at the tips of the branches in swollen conical structures, the **receptacles** (Figs. 156, A; 158). The numerous microsporangia are produced terminally on very small branched filaments arising from inner walls of the conceptacle.

Meiosis occurs in the nucleus of the young microsporangium reducing the number of chromosomes from the diploid number 64 to the haploid

number 32. Thus as a result of meiosis four nuclei are formed, each with 32 chromosomes. These four nuclei may be regarded as equivalent to meiospores, which are not shed directly. They are retained within the microsporangium, where each undergoes a series of four mitotic divisions with the formation of 16 haploid cells. This group of cells may be regarded as a very much reduced gametophyte. Since each of the four nuclei behaves in the same way, there are four of these 16-celled game-

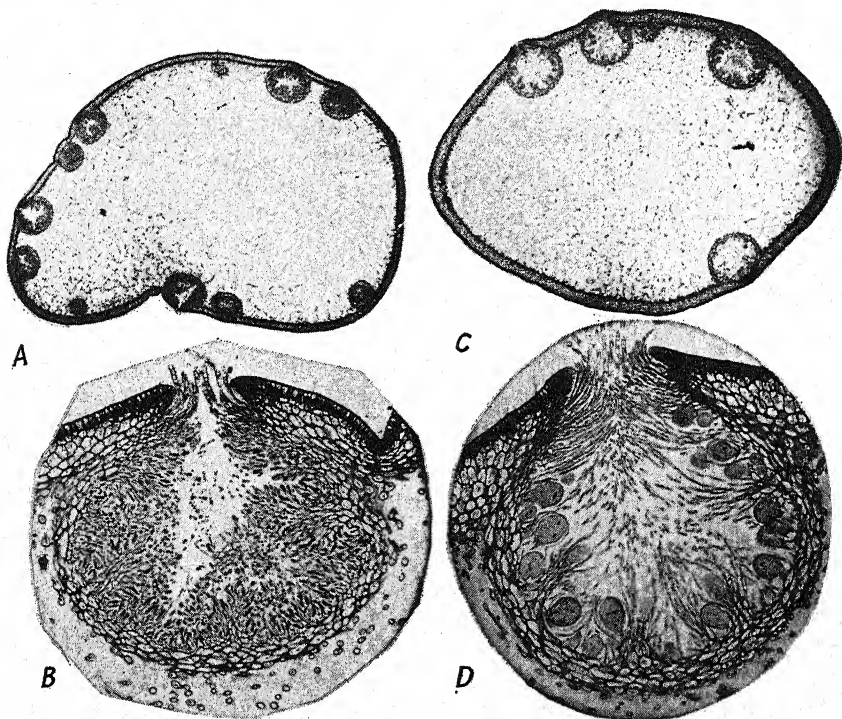


FIG. 158. *Fucus*, sexual reproduction. A, transverse section of a receptacle, showing several conceptacles; B, a conceptacle enlarged, showing numerous microsporangia and sterile hairs, or paraphyses; C, transverse section of a receptacle, showing four conceptacles; D, one conceptacle enlarged, showing numerous megasporangia and sterile hairs, or paraphyses.

tophytes making a total of 64 haploid cells, each of which eventually develops a microgamete, or sperm, with 32 chromosomes. The sperms are minute slightly elongated structures that owe their motility to two laterally attached cilia. At maturity, the sperms escape from the microsporangium and swim to the eggs. Meiosis also occurs in the nucleus of the young megasporangium with the production of four meiospore nuclei, each with 32 chromosomes, the $1N$ number. Again as in the case of the meiospores in the microsporangium, the spores are not shed but are re-

tained in the megasporangium. Through a single mitotic division which immediately follows meiosis, each meiospore forms a small two-nucleate gametophyte. Since in this instance there is only one cell generation in the gametophytic tissue, there is a total of eight nuclei, each with 32 chromosomes. Cleavage walls later divide the cytoplasm into eight blocks, each with one of the haploid nuclei. When these cell masses round up, they become the nonmotile macrogametes or eggs, each with 32 chromosomes. At maturity, they are set free from the sporangium and float in the water. These megagametes, or eggs, are hundreds of times larger than the microgametes, or sperms. The ebb and flow of the tides has an influence on the shedding of gametes. As the tides ebb, the *Fucus* plants are left exposed on the rocks. When the tides flow back, the plants are again submerged. The alternate drying and wetting of the abundant gelatinous material is an aid in the expulsion of the gametes from the conceptacles in which they are formed.

When the gametes are expelled from the conceptacles, the nonmotile eggs floating free in the water are soon surrounded by hundreds of the minute sperms which are attracted to them. The sperms are described as attaching one flagellum to the surface of the egg while the second remains free, lashing the water. The sperms, attached in this way, by reason of their motility set the nonmotile eggs in rotation, which may continue until a sperm penetrates the egg and fertilizes it. The union of the sperm and egg ends the remarkably short haploid, or gametophytic, phase of *Fucus*. With fertilization, the diploid number of 64 chromosomes is restored in the zygote. The zygote, without change of chromosome number, immediately begins to grow and to develop the sporophytic plant that attaches itself to a suitable support, grows into a mature *Fucus* plant, and repeats the life cycle.

The life cycle in *Fucus* is directly opposed to that found in most of the filamentous green algae. The body of *Fucus*, a $2N$, or diploid, structure, is a spore-bearing plant, or sporophyte, while the body of a filamentous green alga, a $1N$, or haploid, structure, is a gamete-producing plant, or gametophyte. In the filamentous green algae, the diploid structure is restricted to one cell, the zygote, and meiosis takes place in this initial cell of the $2N$ phase, *i.e.*, meiosis is initial or zygotic. In contrast to the green algae, an entire $2N$ *Fucus* plant intervenes between the initiation of the diploid condition at fertilization and its termination during meiosis. Compared with the filamentous algae where the gametophyte is relatively large, the gametophytic structures of *Fucus* consist of only a few haploid cells. Meiosis in *Fucus* occurs between the development of diploid and haploid structures. This type is called delayed or intermediate meiosis in contrast with the initial or zygotic meiosis of the filamentous green algae.

The unique feature of reproduction in *Fucus* is the retention of meiospores, their growth forming reduced gametophytes and the eventual formation of gametes within both micro- and megasporangia. The sporangia thus serve both as spore cases and as gametangia. Incomplete observation led to the earlier assumption that the sporangia were sex organs. Even after the facts of the chromosome cycle were known, confusion of terms has persisted resulting in the use of antheridia and oögonia as designations for the micro- and megasporangia. It is now

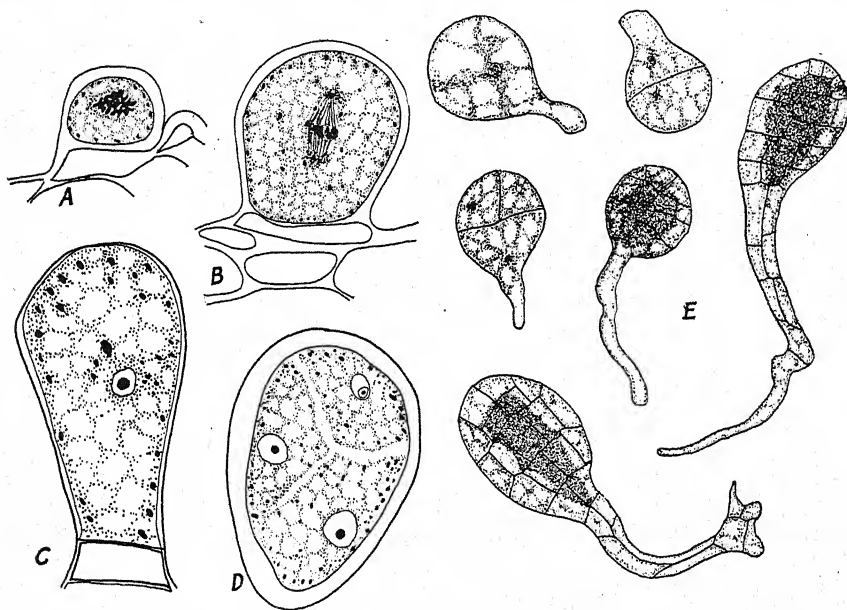


FIG. 159. Development of megasporangia in *Ascophyllum*. A, young megasporangium; B, nuclear division in oögonium reducing the number of chromosomes from $2N$ to $1N$; C, young megasporangium, showing development of basal cell; D, megasporangium, containing four cells, each with $1N$ number of chromosomes; E, *Fucus* sporophytes, showing progressive development from one-celled stage to many-celled plant with small holdfast. (E, drawn by Helen D. Hill.)

recognized that morphologically the reproductive structures of *Fucus* are sporangia and not real sex organs. They have even been compared to the anthers of the flowering plants, which are microsporangia that retain the microspores until the male or microgametophytes are partly developed.

Ascophyllum (Fig. 159), *Pelvetia*, *Sargassum*, and other related genera of brown algae have life histories similar to that of *Fucus*. The essential morphological structures are alike in most respects, and the development of the microsporangia, microgametophytes, and microgametes is essentially the same in all these genera. There is, however, considerable variation in the development of the gametophytic cells and the number of eggs

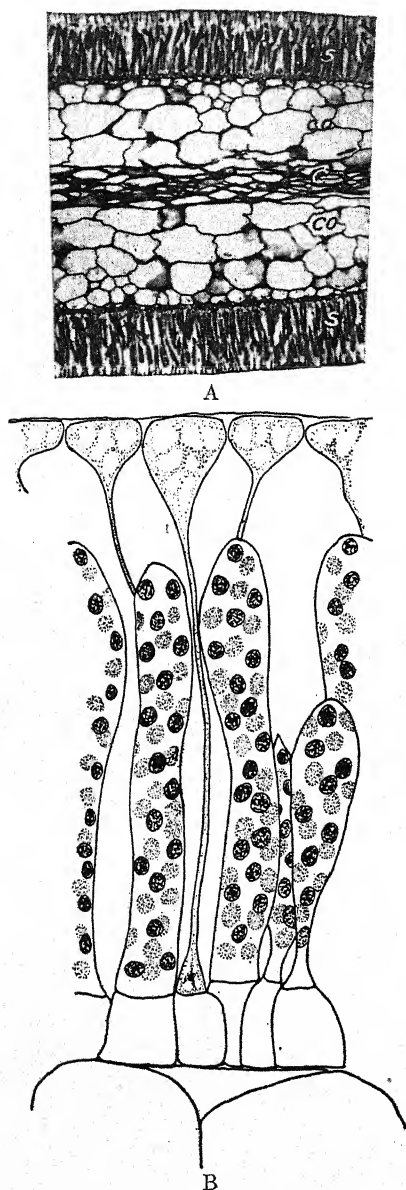


FIG. 160. A, transverse section of a small portion of thallus of *Nereocystis*, showing sporangia, s, at lower and upper layers, also tissue differentiation with a central strand, c, surrounded by a cortical region, co; B, enlarged view of a portion of thallus of *Nereocystis*, showing zoosporangia with zoospores, and paraphyses. (Drawings by Helen D. Hill.)

finally produced in the several genera. Although eight haploid nuclei are always produced from the four meiospores, some of them degenerate. Depending upon the number of disintegrating haploid cells, some genera produce four functional eggs instead of eight as in *Fucus*, others only two, and in certain forms only one.

The Kelps. The methods of reproduction and life histories in the kelps are in general very similar. The life cycle for the genus *Laminaria* is more definitely known than that of others in the group. Late in the growing season, large numbers of single-celled, club-shaped sporangia develop in patches on the surfaces of the blade portion of the thallus. This occurs also in *Nereocystis* (Fig. 160). Associated with the sporangia are slender sterile hairs, known as paraphyses, which have no particular function, although they may serve to protect the developing sporangia. Numerous motile zoospores are formed in the sporangia, escape, and upon germination develop very small branched, filamentous sexual plants. These plants are generally dioecious, *i.e.*, produce but one sort of sex organ, either antheridia or oögonia.

In the sexual plants of the various genera and species of the kelps, considerable diversity in size and form occurs, but all are very small and inconspicuous. The facts of these life histories emphasize the feature of alternating plants with distinctly different functions. There is the large thallus plant body,

which is an asexual diploid plant finally producing spores (zoospores), and the small sexual plant, which produces gametes. There is, therefore, a sporophyte producing spores, alternating in the life cycle with a gametophyte producing gametes.

Zanardinia and Cutleria. Investigation of the life histories of two other genera of the Phaeophyceae has shown very clearly defined alternation of generations. In the genus *Zanardinia*, a Mediterranean form, there are sporophytes, or spore-bearing plants, and gametophytes, or gamete-bearing plants, which, though similar in appearance, differ in chromosome number and alternate with each other in the life history. The diploid sporophytic plant has 44 chromosomes and the haploid gametophyte has 22 chromosomes. The related genus *Cutleria* shows even greater evidence of definite

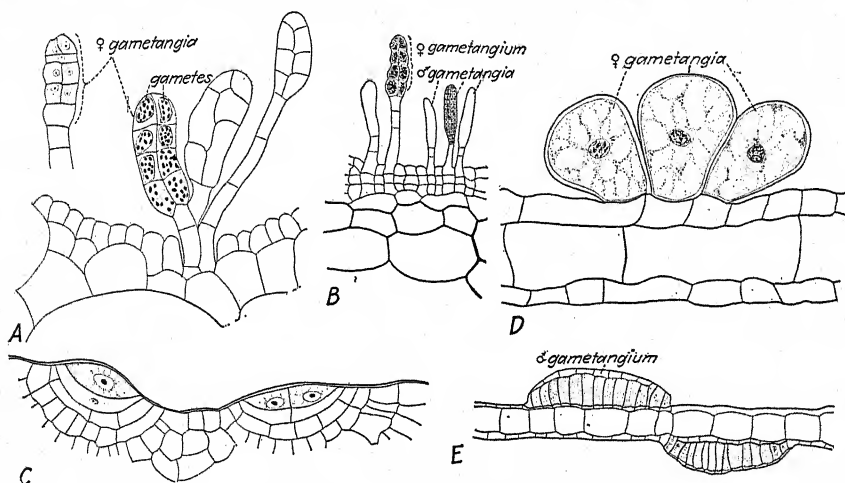


FIG. 161. * Details of sexual reproduction in some genera of the brown algae, as seen in sectional views. A, *Cutleria*, showing the superficial female gametangia containing gametes; B, *Zanardinia*, showing the superficial male gametangia, and female gametangia; C, *Dictyota*, apical region, showing origin of dichotomous branching; D, and E, sexual reproduction in *Dictyota*; D, female gametangia, and E, male gametangia on both sides of the thallus.

alternation of generations. In this genus the two plants, gametophyte and sporophyte, not only satisfy the cytological test of differing chromosome numbers but are different in appearance. The gamete-bearing plant has 24 chromosomes in the nuclei of its cells. In structure the plant is a much branched, ribbon-like body which is attached to the substratum by a holdfast and floats in the water. The spore-bearing plant has 48 chromosomes in the nuclei of its cells. In structure it is a thin, flattened thallus which lies prostrate on the substratum to which it is attached.

In both *Zanardinia* and *Cutleria* the gametangia and zoosporangia are produced on the surface of the plant bodies (Fig. 161, A, B). In each case the sporophyte, which is the diploid, or $2N$, plant, produces zoospores. The zoospores are produced following a reduction division and are characterized by having the haploid, or $1N$, number of chromosomes in their nuclei. These zoospores attach themselves to suitable substrata and by growth develop into the sexual plants without change in chromosome number. When mature, these gametophytic plants produce male and female gametangia in which the heterogametes are developed. When these gametes, which are

haploid, or $1N$, structures, fuse, the number of chromosomes is doubled and the resulting zygote develops into the diploid spore-bearing plant, which is characterized by having the double number of chromosomes throughout its structure. The production of zoospores, following a reduction division, continues the alternating cycle. The investigation, demonstrating the alternation of the two plants with different function and different chromosome numbers, in these genera, is one of the most important contributions to the biology of the brown algae.

SUMMARY OF THE FEATURES OF THE PHAEOPHYCEAE

The class Phaeophyceae, brown-colored because a brown pigment, fucoxanthol, obscures the green chlorophyll in the plastids, is a group of marine algae of wide distribution. Besides the brown color the Phaeophyceae are distinguished by cilia of unequal length generally attached laterally to all motile reproductive cells such as zoospores and gametes. The brown algae are very diverse in form and size, ranging from small filamentous plants like *Ectocarpus*, a few centimeters in length, to the giant kelps. The life cycles of the Phaeophyceae show great variability. There is a definite alternation of $1N$ and $2N$ chromosome numbers associated with the gametophytic and sporophytic structures in all brown algae. In contrast with many green algae, diploid plant bodies that are definitely spore-bearing, or sporophytic, are generally developed. These plants alternate with haploid structures that are gamete-bearing, or gametophytic. In many genera, the sporophytes and gametophytes, although differing in size, are both independent plants. In the group to which *Fucus* belongs, the plant body is diploid and sporophytic, with the alternate gametophytic structures restricted to a few dependent haploid cells.

THE RHODOPHYCEAE—RED ALGAE

General Characteristics. The class Rhodophyceae, or red algae, a large group composed mostly of marine algae, are of world-wide distribution, with the greatest display of species in the warm waters of the tropical, subtropical, and lower temperate zones. Some of the largest forms, however, grow in the colder oceans. The characteristic colors of the Rhodophyceae come from two pigments accessory to chlorophyll. Red algae generally grow attached, mostly to rocks near the shore. Sometimes they live as epiphytes on larger water plants and a few are parasitic on other plants. Though most of the red algae are marine plants, a few grow in fresh water. A favorite habitat of the fresh-water forms is in mountain streams, the outflow of springs, and other locations where there is good aeration of the water.

Form and Structure. Their bright coloration and delicate structure lend great beauty to many of the red algae (Fig. 162). On the whole they are larger than the members of the Chlorophyceae but never attain

the proportions of such brown algae as the kelps. In form Rhodophyceae range from filamentous plants, often heterotrichous, to those with expanded thalli which may be 3 to 4 ft. in length. Some kinds are ribbon-shaped and attain considerable differentiation of tissues. Small cells in an outer layer of the thallus contain chloroplasts and are therefore the seat of photosynthetic activity. A central portion is composed of larger cells. Some slender kinds are composed of several rows of cells appearing as tubes or siphons. The presence of gelatinous material in the thallus is characteristic of most red algae. In the simple branching forms, the filaments are covered with a sheath of gelatinous nature which makes the

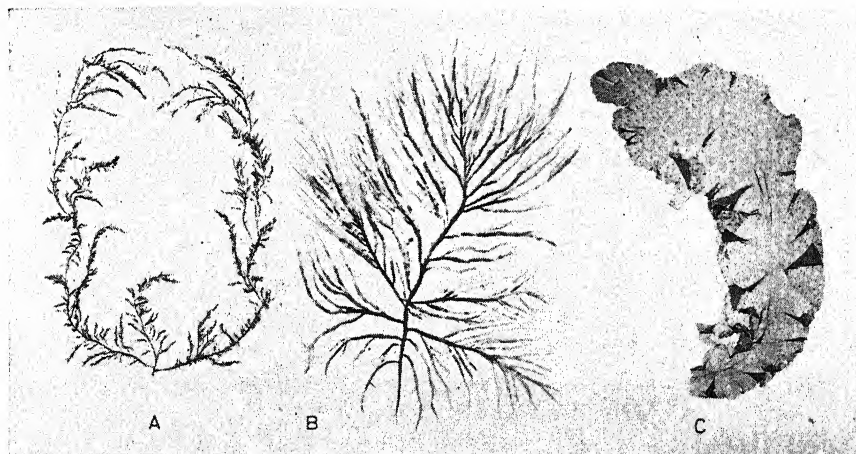


FIG. 162. Some species of red algae. A, *Dasya*; B, *Gardiella*; C, *Grinnellia*.

whole plant slippery to the touch. Agar, a gelatinous substance extensively used as a medium upon which fungi and bacteria are cultured, is prepared from the thalli of some species of the red algae. This substance is also used in articles of diet for invalids and in the preparation of certain medicines. Red algae are extensively used as food by the people of Oriental countries and they are frequently on sale in the markets of coastal cities of the United States. When cooked, they tend to retain both their color and their gelatinous nature.

The red algae have a definite cell structure of high organization. Generally there is a single nucleus although some cells are multinucleate. One or several plastids, which may contain pyrenoids, float in the cytoplasm. The plastids contain the green pigment chlorophyll, various yellow carotenoids, a red water-soluble pigment, **phycoerythrin**, and in some cases, a blue one, **phycocyanin**. The red and blue pigments obscure the green

color of the chlorophyll. The products of photosynthesis are sugars. Food reserves in the red algae may occur as alcohols, but are chiefly stored in the form of a polysaccharide, called **Floridian starch**. Upon treatment with iodine, Floridian starch is said to turn yellow in color, later changing to red, and finally to blue. Conspicuous **protoplasmic connections** that pass through openings or pores in the end walls of the cells are generally found in the tissues of the red algae.

Sexual Reproduction. A unique characteristic of the Rhodophyceae is a total lack of cilia, or flagella, and consequently of motility in all types of reproductive structures. Heterogamous sexual reproduction is general and is achieved by small male cells, or microgametes, and larger female cells, or macrogametes, generally produced on separate plants. The male sex organs are simple, but the female sex organs are unusual structures that are associated with complex accessory tissue. The male sex organs, the antheridia or microgametangia, are simple, single-celled structures produced abundantly in clusters on branches of the vegetative plant body. Each antheridium contains a single male or microgamete called a **spermatium**, which escapes at maturity. The spermatia usually contain a single nucleus, but in a few genera this nucleus divides and forms two nuclei. Since the spermatia lack structures which provide motility, they float in water to the female sex organs.

The female sex organ in the red algae is called the **carpogonium**. This is a complex structure (Fig. 163, *E, F*) consisting of an enlarged or swollen basal portion and an elongated projection termed the **trichogyne**. There is considerable diversity in the form and size of the trichogyne in the various genera. The trichogyne may be cut off from the carpogonium proper by a cell wall or it may be merely a projection of the carpogonium. In those cases where the trichogyne is cut off as a separate cell, it has its own nucleus; in others it may not have a nucleus. The carpogonial cell corresponds in every essential with the oögonium of the green algae. It contains a protoplast, consisting of nucleus and cytoplasm, which comprises the female gamete. The carpogonium is borne upon a branch of the filament called the carpogonial branch, which is composed of several enlarged and specialized cells. When the gametes are mature, the spermatium floats to the female sex organ, where it attaches itself to the trichogyne. After the adjoining portions of the cell walls have been dissolved, the nucleus passes through the trichogyne down to the carpogonium, where it fuses with the nucleus of the female gamete. This constitutes fertilization. In most genera, about the time of fertilization or soon after, certain cells of the carpogonial branch or of filaments adjacent to it fuse with the carpogonium. These cells are called **auxiliary cells** and their function is to aid in nutrition by contributing their protoplasmic contents

to the developing zygote and its associated structures. Following the fusion of the auxiliary cells and the carpogonium, the structure containing the zygote continues development and at maturity produces spores called

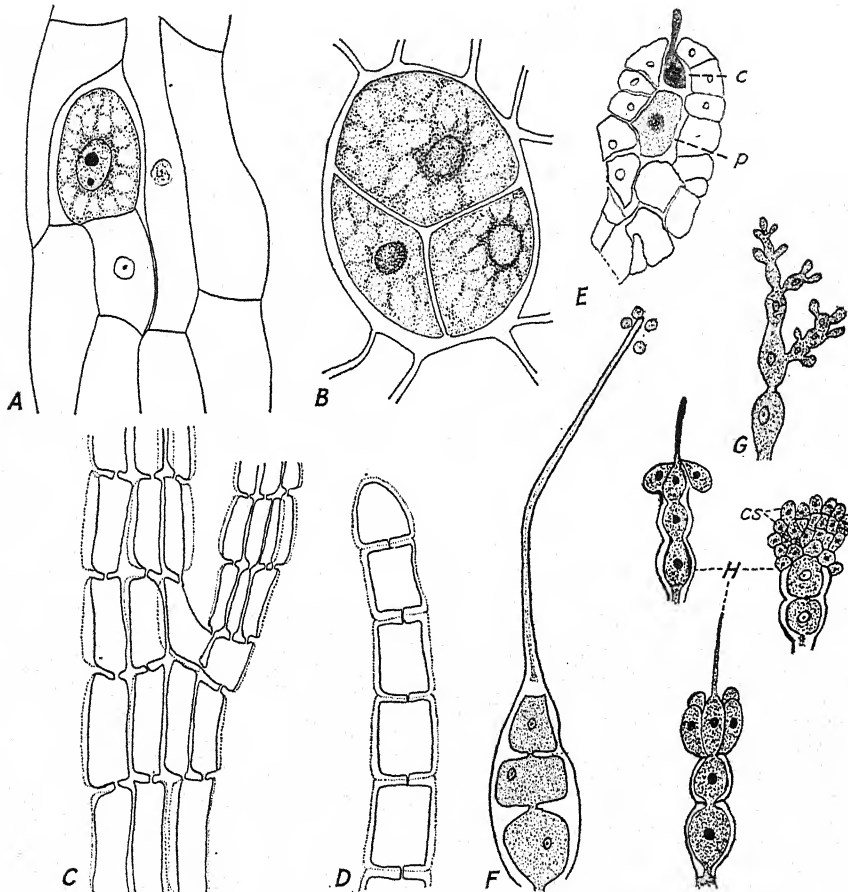


FIG. 163. *Polysiphonia*, showing, A, young sporangium; B, tetraspores; C, portion of plant to illustrate the organization of filaments of several "siphons" and cytoplasmic connections between cells; D, a small portion of filament of *Plumaria*, illustrating cytoplasmic connections between cells; E-H, sexual reproduction in red algae; E, young procarp of *Polysiphonia*; c, carpogonium with trichogyne; p, pericentral cell surrounded by several auxiliary cells; F, *Nemalion*, carpogonial branch, with carpogonium and attached trichogyne with spermatia adhering; G, antheridial branch; H, stages in development of cystocarp and carpospores, cs, following fertilization of egg cell within the carpogonium. (B, C, D, F, G, and H drawn by Helen D. Hill.)

carpospores (Fig. 163, H). The entire structure developed as a result of the stimulus of fertilization is termed the **cystocarp** or "cyst fruit." This has a great diversity of forms in the various genera.

Some Life Histories in the Red Algae. The study of the details of the reproduction of certain genera of the red algae may serve to illustrate the essential features of the life histories of the group.

Batrachospermum, a genus growing in the fresh waters of the north temperate regions, and *Nemalion*, a marine genus, are representative of the lower or simpler red algae. The plants of these two genera are very similar in appearance and structural features, and their life histories agree in all essential respects. The genera are characterized by having plant bodies of delicate, branched filaments ranging in size from a few to several inches in length. The cells of the filaments are united to the adjoining cells by protoplasmic connections, a structural feature characteristic of the red algae.

Nemalion. In *Nemalion* the haploid filamentous plant body has 8 as its chromosome number. There are male and female plants. On the former, the male sex organs, the antheridia, are produced in clusters on tips of very small branches. Each antheridium produces a single microgamete called a **spermatium**. Without cilia, the nonmotile spermatium floats to the female sex organ. The spermatium corresponds in a general way to the sperm but differs from the sperm in the division of its nucleus into two nuclei.

The female sex organ borne on distinct female plants consists of an enlarged cell, the carpogonium, bearing a slender more or less club-shaped structure, the **trichogyne** (Fig. 163, *F*). The carpogonium with its trichogyne is developed terminally on a branch of one to five large basal cells, which collectively are called the **carpogonial branch**. The female or macrogamete is the protoplast within the carpogonium proper. At the time of fertilization, the spermatium attaches itself to the trichogyne, and the contents pass through the cell wall of the latter. One of the two nuclei passes down through the trichogyne and fuses with the nucleus of the protoplast of the carpogonium.

The nucleus of each gamete contains 8 chromosomes. After syngamy the nucleus of the resulting zygote in the base of the carpogonium contains 16 chromosomes. Meiosis is initial, or zygotic, in these simple red algae much as in most filamentous green algae. Through the meiotic divisions the 16 diploid chromosomes are reduced to 8, the haploid number found in each meiospore nucleus. Probably only one haploid meiospore functions. From the carpogonium numerous short filaments are developed. As each one grows, a haploid nucleus, derived by mitotic division from the meiospore nucleus, migrates into the filament. A single haploid spore is formed at the end of each filament. These are called **carpospores**. The mass of filaments with their terminal carpospores is called a **cystocarp** or a cyst fruit. Since the nuclei of the cells in the filaments and the carpo-

spores each have 8 chromosomes, they are new haploid structures produced on the haploid thallus of the female parent plant. Shedding of the carpospores and their germination to form a new generation of haploid plants complete the life cycle. While there are differences in some of the minor details, the life cycle of *Nemalion* may be regarded as typical for the filamentous red algae such as *Batrachospermum* and others.

Polysiphonia. One of the higher red algae, *Polysiphonia*, has a plant body composed of from 5 to 13 united siphons, or filaments (Fig. 163, A-C). These filaments have the protoplasmic connections between the cells, which are characteristic of red algae. Relatively, the plants are small, from a few to several inches in length. *Polysiphonia* plants are of three kinds. There are male plants which produce the male or microgametes and female plants which bear the female or macrogametes. Since these male and female plants produce gametes, they are gametophytic. Besides these, there are similar plants that never produce gametes but always develop spores. The spores are borne in sporangia in groups of four and hence are called **tetraspores** (Fig. 163, B). These spore-producing plants are sporophytic.

The plants differ not only in that one kind produces gametes and the other spores but also in chromosome numbers. These two types alternate in the life cycle of the organism. The male and female plants have 20 chromosomes in the nuclei of their cells and represent the $1N$, or haploid, phase. The sporangial plants producing tetraspores have 40 chromosomes and are diploid. The haploid male and female plants grow from the tetraspores that have 20 chromosomes. The diploid sporangia-bearing plants grow from carpospores with 40 chromosomes that are produced as a result of the fertilization processes.

The antheridia of *Polysiphonia*, produced in very dense clusters on branches of the male plants, are in all essentials like those described for *Nemalion*. The spermatia are uninucleate and in this respect are more typical of the red algae than are the binucleate spermatia of *Nemalion*. The female sex organ, or carpogonium (Fig. 163, F), with its trichogyne is produced on a branch consisting of three or four cells. This branch is the carpogonial branch. Certain adjacent cells are known as the auxiliary cells. After the spermatium has attached itself to the trichogyne, the contents pass into it and the nucleus of the spermatium unites with the nucleus of the carpogonium. Each of these nuclei has 20 chromosomes, the haploid, or $1N$, number. The diploid number in the zygote, resulting from fertilization, is therefore 40, the $2N$ number. After fertilization, certain cells of the filaments of the female plant, called the auxiliary cells, the function of which is of a nutritive nature, also fuse with the carpogonium. Generally about seven auxiliary cells fuse with the carpo-

gonium, each contributing its nucleus and cytoplasm. There is, however, no further fusion of nuclei in this complex structure. The zygote now undergoes several mitotic divisions in rapid succession without changing the diploid (40) chromosome number. The events just described result in the production of a structure which contains several diploid nuclei, each with 40 chromosomes, which have originated from the division of the zygote without change in chromosome number, and several haploid nuclei with 20 chromosomes, the nuclei of the auxiliary cells. These nuclei with the cytoplasm and food materials of their cells are enclosed within a single wall. Soon there appear short branches into which the diploid nuclei migrate as they form. The ends of the branches produce carpospores. These carpospores each contain nuclei with 40 chromosomes, the diploid number. As this structure develops, certain cells of the adjacent filaments begin to grow and envelop it. This enveloping growth results in the production of an urn-shaped structure of haploid tissue, which contains the mature diploid carpospores. The entire structure is called a cystocarp. This structure differs from the cystocarp of *Nemalion* in that it has a covering and, more important, in that the carpospores have the diploid number of chromosomes instead of the haploid, as was the case in *Nemalion*. When the carpospores are mature, they escape from the urn-shaped cystocarp and, upon germination, produce the sporangial plants. The plants so produced have 40 chromosomes in the nuclei of their cells and are therefore diploid structures. These diploid plants do not produce sex organs. They produce sporangia which are borne on short stalk-cells branching from the central siphon of the plant (Fig. 163, A, B). As a sporangium develops, the nucleus of its protoplast undergoes meiosis and four meiospores are formed each with the haploid number of 20 chromosomes. These are the tetraspores. The haploid tetraspores germinate and develop into male and female plants each with 20 chromosomes, completing the life cycle. Thus gamete-producing haploid plants with 20 chromosomes alternate in the life cycle with spore-producing diploid plants with 40 chromosomes. The two compensating processes, fertilization with union of gametes and meiosis, at critical points in the life cycle keep the chromosome numbers in equilibrium from generation to generation.

Asexual Reproduction. Besides their diverse methods of sexual reproduction most red algae also have methods of asexual multiplication. One of the most common methods is the formation of a single-celled structure called a **monospore**, produced in a sporangium without change in chromosome numbers. When shed, the monospore germinates and grows into a new plant. Monospores are generally produced on the haploid plants and serve to multiply the individuals in this phase. Besides monospores

there are **bisporos**, produced two in a sporangium, and **polysporos**, with many in a sporangium. Another term, **parasporos**, is also applied to some of the asexual reproductive cells. The cytology of development in these types of spores is not completely understood. Possibly, **bisporos** are merely monospores that have divided. Since diploid plants normally bearing tetrasporos sometimes produce polysporos or parasporos, some investigators have considered these asexual reproductive cells as derivatives of the tetrasporangia. Perhaps the production of all these kinds of spores should be regarded as nonsexual methods of multiplication accessory to sexual reproduction, occurring regularly in the life cycle.

Summary of the Rhodophyceae, or Red Algae. The presence of red color in addition to green chlorophyll in the plastids, protoplasmic connections between the vegetative cells of the plant body, and considerable differentiation of cells are outstanding structural features of the group. Sexual reproduction is of a complex heterogamous type accompanied by the formation of complicated sex organs. The total absence of any motile reproductive cells is a unique characteristic in an aquatic group. The presence of a definite alternation of haploid gamete-producing plants with diploid spore-producing plants establishes the alternation of chromosome numbers in the higher genera of red algae. Diversities in form, habitat, structure, and reproduction are illustrated in *Batrachospermum*, *Nemalion*, and *Polysiphonia*.

CHAPTER 15

THALLOPHYTA—BACTERIA, SLIME MOLDS, FUNGI

BACTERIA

General Characteristics. Bacteria are microscopic unicellular organisms, which are often known as “germs” and “microbes.” Their relationship to other living things is very obscure. In their unicellular structure, in the absence of a definite nucleus, and in their entirely asexual methods of reproduction, they show similarities to the blue-green algae, and along with them they are often set apart in a single group known as the **Schizomycetes**. They differ from the blue-green algae in that their cells contain no chlorophyll, and therefore they are unable, with the exception of a few species, to manufacture their own carbohydrate foods. On this point they agree with the fungi. Their inability to manufacture their own carbohydrate foods makes it necessary for them to grow where these foods are present. Some species are **parasites**, attacking the living cells of other plants or of animals and securing their foods from that source. Most bacteria grow on the dead remains or the products of plant and animal life without a direct relationship with living cells and are, therefore, **saprophytes**. Parasitic bacteria are responsible for some of the diseases of plants and animals, while the saprophytic kinds may be very beneficial.

While most of the bacteria are heterotrophic (dependent) plants, a few species are autotrophic, *i.e.*, they are capable of synthesizing carbohydrates out of carbon dioxide and water and hence can make all their own foods. Some of these, such as the purple bacteria, contain green pigments (bacteriochlorophyll) and can carry on a type of photosynthesis, while others, such as the hydrogen bacteria, iron bacteria, nitrifying bacteria, and some of the sulfur bacteria, lack green pigments but can manufacture carbohydrates by chemosynthesis (see Chap. 5).

The study of bacteria has developed into an independent science known as bacteriology. The group is relatively not a large one, comprising less than a thousand species. Only a brief treatment of the bacteria can be given here.

Size and Distribution. Bacteria are the smallest of all known living things. The largest of them measure about $\frac{1}{10}$ mm. ($\frac{1}{250}$ in.) in greatest dimension and are nearly large enough to be visible to the unaided eye.

The smallest known are $\frac{1}{10} \mu$ ($1/10,000$ mm. or $1/250,000$ in.) in length. This means that, if they were placed end to end, it would require 250 of the largest kind and 250,000 of the smallest kind to make a chain 1 in. long. The rod-shaped forms average about 2μ in length and $\frac{1}{2} \mu$ in width ($1 \mu = 0.001$ mm.). Thousands of bacteria might be contained in a single drop of water and not be at all crowded for space. A cubic centimeter (20 to 30 drops) of sour milk contains many millions of them. Not all substrata are suitable for the growth of bacteria. They may be present on any exposed surface that does not possess properties fatal to their existence. In many such situations they are unable to multiply and

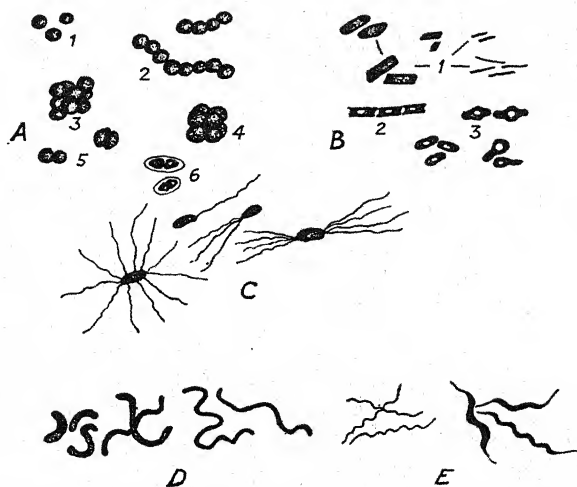


FIG. 164. Forms of bacteria. A, spherical forms; 1, coccus; 2, streptococcus; 3, staphylococcus; 4, *Sarcina*; 5, diplococcus; 6, encapsulated diplococci; B, nonflagellated bacilli; 1, types, shapes, and groupings of bacilli; 2 and 3, bacilli showing various positions of endospores; C, flagellated bacteria; D, types of spirilla; E, spirochaetes. (Drawn by Dr. R. D. Reid.)

hence their numbers do not increase. On or in a substratum suitable for their growth and development they may become extremely numerous. Decaying vegetable and animal materials and solutions rich in organic matter are usually excellent places for the growth of saprophytic species.

Shape and Form. In shape or form, two principal types of bacteria may be differentiated, *viz.*, the spherical, or globose, forms and the cylindrical (Fig. 164). The spherical forms are called *cocci* (singular *coccus*) and are classified into several groups based mainly on the manner in which they remain together after dividing. If they divide in only one plane, they may remain in pairs, in which case they are called *diplococci*, or they may cling together in chains. The latter are called *streptococci*. Some forms divide in two planes and cling together in irregular masses shaped like bunches

of grapes. Such forms are called **staphylococci**, or **micrococci**. Still others divide in three planes and form cubical groups. These are placed in the genus *Sarcina*. Coccus forms are often distorted into oval or elliptical shapes.

The cylindrical types may consist of straight, rod-like forms collectively called **bacilli**, or the rods may be curved, as in the genus *Vibrio*, or spirally twisted. Those with rigid spirals consisting of one or more complete turns are placed in the genus *Spirillum*, while those with flexible spirals are called **Spirochaetes**.

Under certain conditions not well understood, a bacterial cell of one of the foregoing types may alter its shape to some unusual or abnormal form. Such alterations are not uncommon in some species and the altered cell shapes are known as **involution forms**.

Structure of the Bacterial Cell. Owing to the very minute size of the bacterial cell, its structural features have been very difficult to determine. Studies with the electron microscope have thrown some light on these features and may in the future provide a better understanding of the cytology of bacteria. The presence of a definite cell wall in some species has already been indicated. Whether or not there is always a definite cell wall present, there is always at least an outer limiting membrane which can be demonstrated by plasmolyzing the cell. This membrane, or wall, in some species is surrounded by a thin gelatinous sheath, or **capsule**, somewhat of the nature of the sheath present in many of the blue-green algae. This sheath swells in aqueous solutions and makes the solutions slimy in character. The living content—protoplast—of the cell is apparently of very simple and primitive character. The cytoplasm contains granules of various sorts. Among them are what appear to be chromatin granules which may represent the nuclear matter of the cell. No definite nucleus with a nuclear membrane is present. The protoplast contains no chlorophyll and the bacterial cell is in most cases entirely colorless, although a few species contain coloring compounds, mostly of red and purple hues.

Some bacteria are motile by means of cilia or flagella. Sometimes a single terminal flagellum is present; sometimes there are two or more at one or both ends, and in some species they are numerous on all sides of the bacterial cell. The coccus forms have no cilia or flagella; most of the spirillum types are flagellated; of the bacillus types, some have flagella and some do not.

The Gram Reaction. Two different kinds of bacteria are commonly differentiated on the basis of their response to a differential stain originally devised by the Danish investigator Gram. The stain consists of a crystal violet solution and an iodine solution. Those species of bacteria which retain the stain are called **Gram-positive**, while those which do not are called **Gram-negative**. This differential staining is widely used by bacteriol-

ogists in the study and identification of bacteria. Furthermore, Gram-positiveness and Gram-negativeness are associated with other properties of the bacteria such as sensitivity to dyes and antibacterial substances, a knowledge of which is important in methods of control.

Reproduction. Multiplication of bacterial cells is apparently accomplished only by the process of cell division. Whether or not this is a primitive form of mitosis has not been definitely determined, but both mitosis and direct cell division or fission are said to be present in the group. It is a rapid process, occupying usually about 30 min.; but when in vigorous condition, some species are said to divide as often as every 20 min. It has been calculated that, if division occurs only every hour, the descendants of a single cell after 24 hr. would number 17 million individuals and that in 2 days the number would reach 281 billions of individuals.

Spore Formation. Under certain conditions, changes take place in some bacterial cells which result in the formation of bodies called spores, in which the vital activities of the protoplasm are retained. Only two genera of bacteria, *Bacillus* and *Clostridium*, form spores. Both are rod forms. Usually but one spore is formed in each bacterial cell. These spores are always nonmotile. They differ from the usual bacterial cell in their capacity to resist prolonged unfavorable external conditions, such as drought, high or low temperatures, and disinfecting chemicals, and in their reaction with certain staining solutions. Some spores withstand as much as 16 hr. of constant boiling. On the return of favorable conditions, these spores will germinate, assume the original form of the bacterial cell, and soon grow to normal size for the species. Spore formation is not to be considered a method of reproduction or of multiplication, since but one spore is formed in each bacterial cell and but one new bacterium comes from each spore. It may be regarded as a stage in the life cycle of the organism.

Economic Importance of Bacteria. *Fermentation and Decay.* Many saprophytic species of bacteria are capable of producing profound chemical changes in the substrata on which they grow. The decay of plant and animal bodies and the process known as fermentation are changes of this type. Decay is the more comprehensive term and includes the decomposition of organic bodies into their constituents or into such simple compounds as water, carbon dioxide, ammonia, and hydrogen sulfide. When an abundant supply of oxygen is not available, as in the decay of the bodies of the larger animals in which nitrogenous materials are abundant, unpleasant odors are often developed, and the process is known as **putrefaction**. The processes of decay are important to man from at least two standpoints. They prevent the accumulation of organic matter, both plant and animal, on the earth, and they result in the formation of simple compounds or set free elements that are returned to the soil to be used again by plants.

Many of the fermentation processes that are carried on by bacteria are of

household or commercial importance. Thus species of *Acetobacter* produce acetic acid (vinegar) from the alcohol formed from the juice of ripe fruits, especially apples and grapes. The alcohol itself is formed in a similar fermentation process by different organisms (yeasts) acting on the carbohydrates in the fruit juices. Processes of this type have already been discussed in Chap. 12 of this book. The souring of milk is another fermentation process that involves the conversion of sugar of milk (lactose) into lactic acid. The making of dill pickles, the manufacture of cheeses, the making of sauerkraut, the retting of flax, and the tanning of leather are other examples of fermentation processes of commercial importance.

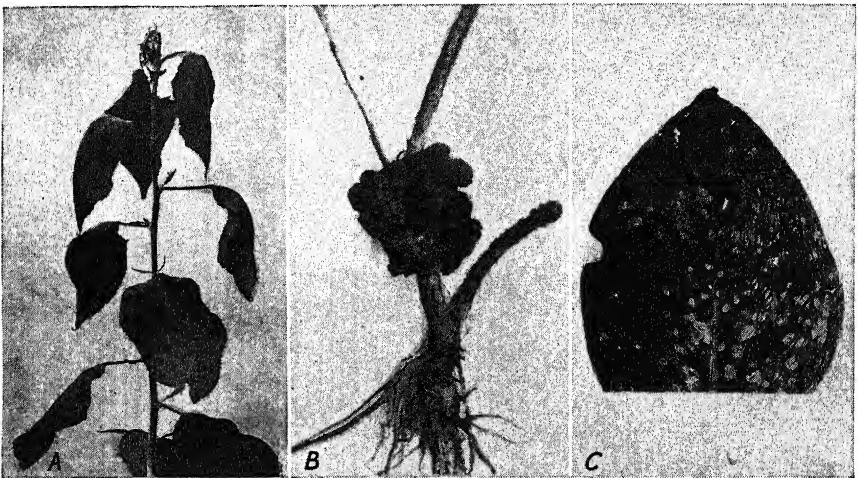


FIG. 165. Bacterial diseases. A, the "fire-blight" disease of apple; leaves and tips of twigs suddenly wilt and die, the terminal portion of the twig usually curling over; B, the "crown-gall" disease on rose; woody gall-like growths are formed at the base of the stem; C, the "wild-fire" disease of tobacco; small circular dead areas are formed on the leaves.

Some of the methods of sewage disposal are dependent for their efficiency on the activities of bacteria. This is especially true of those methods involving the use of septic tanks and cesspools. Certain bacteria rapidly break down the solid organic materials into soluble compounds. Likewise the use of sand filters for sewage disposal involves the action of bacteria, mostly of the aerobic types.

Bacteria and Soil Fertility. Of all the living organisms found in soils, bacteria are among the most active. It is not unusual to find a hundred million or more individual bacteria per gram of soil. They are especially abundant in the surface layers of soil, decreasing in numbers with depth of soil. These bacteria, along with other soil organisms, play a dominant role in soil fertility. In general, they succeed in converting insoluble or un-

available materials into forms that can be used by higher plants. Among the simpler compounds they produce are carbon dioxide, ammonia, nitrates, and sulfates. The processes involved in nitrogen transformations, including ammonification, nitrification, denitrification, and nitrogen fixation, have already been considered in Chap. 7. The bacteria that bring about decomposition of cellulose and similar compounds are important in the production of humus. Among the soil bacteria there are anaerobic and aerobic forms, autotrophic as well as heterotrophic species.

Bacteria as Disease-producing Agents. As stated on a previous page, only the parasitic species of bacteria are capable of causing disease in other organisms. Not all diseases of either plants or animals are caused by bacteria. Many plant diseases are caused by fungi. "Fire blight" of apple and pear trees (Fig. 165, A), "crown gall" of various fruit trees and ornamental plants (Fig. 165, B), and "wildfire" of tobacco (Fig. 165, C) are examples of bacterial diseases of plants. Certain types of decays of parts of such herbaceous plants as cabbage, celery, and various members of the root crops often become serious under storage conditions owing to the presence of bacteria. Likewise, many animal diseases are directly traceable to bacteria, notable among them being tonsillitis, erysipelas, diphtheria, tuberculosis, typhoid, pneumonia, and cholera.

VIRUSES

There are some diseases of plants, commonly called "mosaics" or "yellows," that can be transmitted from one plant to another by means of sap from diseased plants that has been passed through a porcelain filter so fine as to remove completely even the smallest bacteria. The causal agents of such infectious diseases are so small as to be invisible even under the highest power magnifications of compound microscopes. Because they are able to pass through bacterial filters, they have been called **filterable viruses**. Many diseases of human beings are also caused by viruses, among them rabies, smallpox, infantile paralysis, measles, yellow fever, chicken pox, influenza, and common colds.

Viruses cannot be made to multiply on artificial media, but multiply readily in living cells. They can be precipitated out of suspensions by chemical means without losing their activity. Some of them have been isolated in a pure form and even crystallized. All thus far isolated have been found to be proteins of very large molecular size and weight. There are many different kinds of viruses and apparently different races or strains within a type.

Whether the viruses are living organisms, as originally believed, cannot be stated with certainty. In their ability to reproduce themselves in living tissues they resemble microorganisms. No one has ever succeeded,

however, in demonstrating that they carry on respiration or have a metabolism. Certainly those viruses which have been prepared in pure crystalline form and found to be proteins are not living organisms in the ordinary sense.

ACTINOMYCETES

The Actinomycetes are a group of microorganisms, some of which are mold-like and others bacteria-like. For this and other reasons they are difficult to classify. Some authors place them with the Fungi Imperfecti; others consider them as an independent group of fungi; still others classify them with the bacteria in a separate order, the Actinomycetales. Only a brief mention can be given them here.

The Actinomycetes differ from nearly all true fungi in the extreme fineness of their mycelia, the hyphae or individual threads of which are commonly only about $1\ \mu$ in diameter. The mycelium, or vegetative plant body, in those forms in which it is well differentiated, is branched and sometimes twisted and curled. The protoplasm of the young hyphae appears to be undifferentiated, but the older parts of the mycelium show definite granules and vacuoles. Nuclei have been reported to be present in some species. The mycelium in some species commonly breaks up into small fragments called **arthrospores**, which often look like bacterial cells and which might easily be mistaken for the latter. Many species also produce asexual spores, called conidia, on aerial hyphae, which appear as a fine powdery coat on the surface of cultures. The conidia-bearing filaments are often spirally twisted.

The spores of Actinomycetes seem to be widely distributed in the atmosphere. An agar plate exposed to the air will often yield small, round, flat colonies of these organisms closely adherent to the medium, often highly colored and emitting a penetrating musty odor. The production of pigments is one of the most striking cultural characters of the group. The spores are often white or gray; the mycelium may be nearly colorless or may be colored red, orange, yellow, green or blue. In addition, soluble pigments may diffuse out into the medium. These may be of the same color as the mycelium or different. Many species produce a characteristic brown discoloration of agar.

Like the fungi and most of the bacteria, the Actinomycetes are all either saprophytes, obtaining their food from dead organic matter, or parasites, living on other living organisms. The saprophytic species are widespread in soil and take an active part in the decomposition of complex organic matter, breaking down such compounds as proteins, starch, cellulose, chitin, and perhaps lignin. Most of them are able to reduce nitrates to nitrites but not to ammonia or free nitrogen. Several species are parasitic

on higher plants, causing such diseases as the common potato scab. Others cause spoilage of nuts and of other food and dairy products. Still others cause diseases of animals and man. The term "actinomycosis" is commonly applied to such diseases. Actinomycosis occurs in many wild and domestic animals as well as man. One of the commonest of these diseases is "lumpy jaw" of cattle caused by *Actinomyces bovis*. In man, actinomycosis may involve all parts of the body.

From what has been said in the preceding paragraph it is obvious that the Actinomycetes are of considerable economic importance. The importance of the group has increased since the discovery that some of the species produce antibiotics. Thus streptomycin, which is now being used in medicine to combat certain bacterial diseases, is obtained from *Streptomyces griseus*.

MYXOMYCETES

Introduction. The Myxomycetes, sometimes known as slime molds or slime fungi, constitute a group of doubtful taxonomic position. There is some question as to whether or not they should be regarded as plants, since they resemble plants only in their reproductive stages, while in their vegetative existence the body is a naked, slimy, protoplasmic mass, creeping over the surface of or within the substratum by amoeboid movements. This character at one time earned for them the name *Mycetozoa*, which means "fungous animals" or "animal fungi."

There are approximately 300 species of Myxomycetes. Most of them are saprophytes, creeping over the surface of damp wood, rocks, grass, and other objects in dark moist places in the forest or occasionally, in wet seasons, found on lawns or wherever rotting wood or decaying vegetable matter occurs. A few parasitic species usually included in this group have been transferred to the Phycomycetes by some authors.

The Vegetative Stage (Plasmodium). The spores of the Myxomycetes are non-motile, unicellular bodies formed in profusion in structures called sporangia. The vegetative stage of a Myxomycete begins with the germination of these spores. Germination occurs only when water is present. Each spore emits usually a single, minute, naked mass of protoplasm containing a nucleus. This mass begins to assume amoeboid movements a few minutes after emerging. At one end of the mass a flagellum is differentiated and the whole structure is termed a **swarm spore**, a myxamoeba, or an amoeba (Fig. 166). Soon the swarm spores begin to divide. This division is mitotic. It may occur repeatedly in each of the swarm spores that are formed. One investigator has reported that, by these repeated divisions, a single swarm spore may divide successively into as many as 300 swarm spores in 3 days. In this process of division, the flagellum is retracted but appears again on each of the resulting swarm spores. While the swarm spores may move about by means of these flagella they may also at any time assume amoeboid movements by thrusting out protoplasmic projections known as **pseudopodia**, into which the remainder of the protoplasm flows. If conditions become unfavorable, the individual swarm spores may become quiescent, surround themselves with a definite wall, and enter an encysted or resting stage. On the return of favorable conditions the protoplasm bursts through the encysting wall and again emerges as a swarm spore.

Sooner or later the swarm spores lose their flagella permanently and begin to coalesce or fuse in pairs. These fusions involve also a nuclear fusion and the resulting body is

probably to be considered a zygote and the swarm spores are really gametes. These zygotes then fuse in large numbers but without nuclear fusions. This is the beginning of **plasmodium** formation. A young plasmodium seems to exert an attractive force over the zygotes in the vicinity, for they creep to the plasmodium and fuse with it, thus increasing its size. A plasmodium is thus essentially an aggregation of nucleated protoplasm without either internal or external walls. In other words, it is a coenocytic protoplasmic mass, very soft and slimy in texture, and resembling the white of an egg. It may be either colored or colorless. In this condition the plasmodium creeps over the surface of its substratum, most frequently in positions away from the light. Its method of advance is the same amoeboid motion present in the swarm spores. Pseudopodia are thrust out, often several in a parallel or radiating series from one edge of the plasmodium. The flow of protoplasm is not, however, continuous in one direction. Rather, it might be compared with the continual advance of a rising tide on the beach. There is a definite surge in a forward direction, lasting for a minute or more. Then a reverse movement sets in along the same channel. The forward movement always is of longer duration than the backward movement so that the result

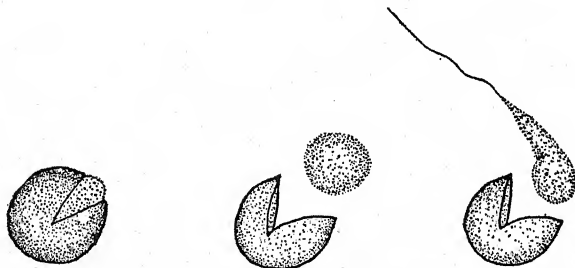


FIG. 166. A germinating spore of a Myxomycete, showing how the protoplasmic mass escapes from the spore wall and differentiates at one end, a long slender flagellum. (After Gilbert, in *Amer. Jour. Botany*, 15: pl. 21.)

is an advance in the former direction. As it advances, it leaves a slimy trail over the surface of the substratum. After this dries down to a thin delicate membrane, one can often trace the path of the plasmodium from the place of its origin to its place of fruiting. In its advance it is continually engulfing such particles of food material as it meets.

The Fruiting Stage (Sporangia). While the plasmodial stage is usually found in dark places, the spores are usually formed in more exposed situations. In general, when it is ready to enter the reproductive stage, the plasmodium comes out to better lighted situations. It may ascend the side of a stump (Fig. 167, A) or, emerging from the dead leaves or other debris on the ground, it may ascend the stems of grasses, small trees, dead sticks, or other nearby objects (Fig. 167, B) on which it elevates itself and thus secures a better distribution of the spores. A few species spend the plasmodial stage in the crevices of old logs and stumps and come to the surface of the same substrata, where the sporangia are formed (Fig. 167, C).

The sporangial stage shows much more variation among species than does the plasmodial stage. For this reason, it is difficult to give a simple account that will suffice for all species. The protoplasm of the plasmodium may pile up into one or more dense cushion-shaped or puffball-like masses, sometimes an inch or more in diameter, on the surface of the substratum; or, in its effused condition, it may form many small separate

sporangia on longer or shorter stalks. The stalk forms first as a denser and erect or columnar body of protoplasm. Over the outside of this small stalk, a portion of the nearby protoplasm climbs or flows, losing water and becoming more compact as it piles up at the apex. This more compact apical mass is the young sporangium. A well-developed, though fragile, membrane-like wall is formed over the surface of the sporangium. Eventually the internal protoplasm becomes divided by cleavage furrows into blocks, at first of large size, and these in turn become subdivided into smaller units until usually uninucleate blocks result. Each of these final units rounds up, secretes a definite and often spiny or otherwise sculptured wall, and becomes a spore. While this is taking place, and even before cleavage is initiated, there also begin to appear in the protoplasm, by processes too complicated to describe here, the formation

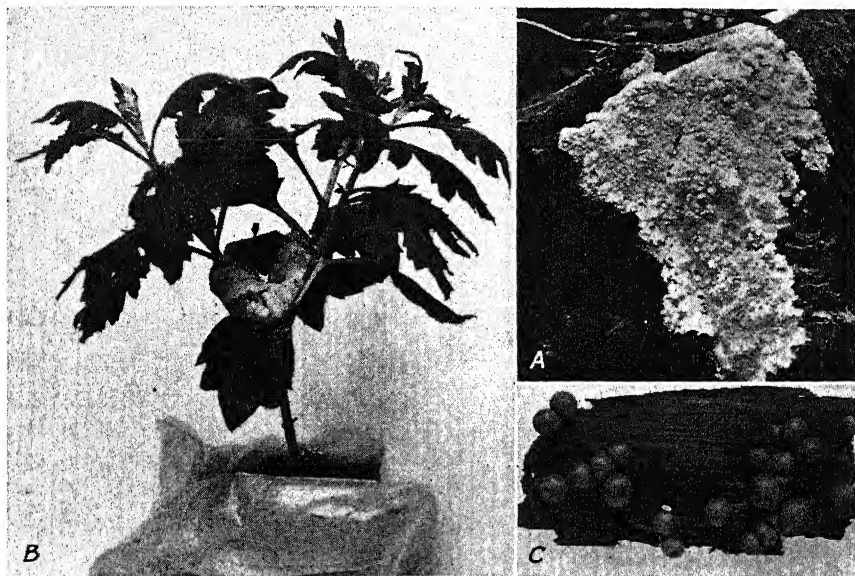


FIG. 167. Sporangial stages of three different species of Myxomycetes. A, very young sporangial stage on side of stump; B, sporangium produced in the forks of *Chrysanthemum* plant which it has climbed; C, sporangia on the surface of an old log.

of definite tubular, simple or branched threads, termed the *capillitium*. This capillitium forms a network through the sporangium, adding to its strength, and, because of its hygroscopic nature, eventually aiding in the dispersal of the spores. Finally, the sporangial wall breaks and the spores are scattered, to begin again the life cycle here described.

FUNGI

GENERAL CHARACTERISTICS

Introduction. The group of plants known as the fungi is an extremely heterogeneous one, comprising at present approximately 70,000 described species, with many thousands more yet to be described. Such kinds as

mushrooms, toadstools, molds, mildews, rusts, and smuts are more or less familiar to everyone, but thousands of others are so minute or so evanescent or grow in such obscure and unfrequented situations that they are to be found only by those trained in the search for them. Their habitats are also extremely diverse. Some are entirely subterranean; others are epiphytic on various other types of plants; one or more species are to be found as parasites on practically every species of higher plants; they grow on human food and in drinking water; in fact, no group of similar size is so omnipresent or so omnivorous, and the economic losses they cause are out of all proportion to their size and importance as plants.

These diversities render difficult an exact statement of the characteristics of the group. One feature they have in common is their universal lack of chlorophyll and hence their inability to manufacture their own carbohydrate foods through the agency of sunlight. They are therefore all either **saprophytes**, obtaining their food from dead organic matter, or **parasites**, living on other living organisms. The organism on which a parasite feeds is known as the **host**. The presence of a parasite may cause abnormal physiological activity within the host that is correctly designated as a **disease**. The parasite in this case is commonly referred to as a **pathogen** and the host as a **suscept**. While the fungi are unable to make carbohydrates out of carbon dioxide and water, they can synthesize fats, proteins, and many other organic substances. In their inability to synthesize carbohydrates they contrast strongly with the algae and agree with the bacteria. The bacteria differ, however, in the lack of a nucleus in the cell, in methods of growth, in reproduction, and in other ways. In form, structure, and functions of the vegetative plant body and in methods of reproduction, the fungi are comparable with the algae and are typical thallophytes.

The Plant Body. The life history of most fungi consists of two phases that are somewhat better differentiated than in the algae. These are a vegetative stage or period, in which the fungus grows through the substratum and builds up a vegetative plant body, and a reproductive stage or period, in which it produces spores or other structures by which the plants are multiplied. To make clear this essential difference between these two phases of the life history, we may examine the ordinary mushroom of commerce. The conspicuous part of this fungus, *i.e.*, the mushroom itself, is the reproductive body. Examination of the interior of the bed from which this mushroom grows reveals a multitude of fine white threads that collectively constitute the **mycelium** or **spawn**, as it is commercially known. This is the vegetative stage of the fungus. Pieces of the spawn planted in the bed grow rapidly, permeate the entire bed, and finally emerge at definite points to form the mushrooms. The latter

are the fruiting structures of the plant and, in fact, are usually spoken of as the fruit bodies or **sporophores** or, more commonly, the mushrooms. It must not be forgotten, however, that the mycelium is just as much an essential part of the plant body as is the mushroom that springs from it.

The Vegetative Phase—Mycelium. *Origin, Structure, and Growth.* With the exception of a few unicellular fungi, all species have a more or less extensive mycelium. In many ways this mycelium (Fig. 168) does not differ materially from the plant body or vegetative system (filament) of an alga, except in the lack of chlorophyll.

The mycelium originates through the germination of a spore. The spores of fungi are similar to those of algae. The simplest spores are unicellular bodies of microscopic size, containing a nucleus and cytoplasm. They may or may not be motile. A spore germinates by pushing out, from a thin place

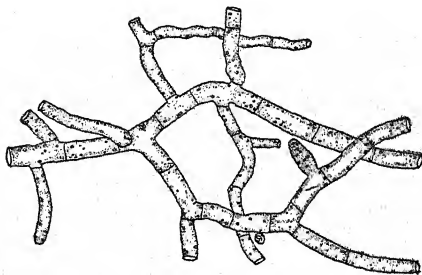


FIG. 168. Small portion of a typical mycelium, showing branching, septation, and the granular cytoplasm. (Drawn by Edna S. Fox.)

in its wall, a tube-like or filament-like process known as a **germ tube** (Fig. 171, *B*). By rapid elongation, accompanied by branching, the mycelium is formed. Growth is more or less localized at the tips of the mycelial branches and is made possible by the absorption of foods from the substratum directly through the cell walls. Cross walls may or may not be formed. Their absence in one large group of the fungi results in a coenocytic type of plant body which is just as characteristic of that group (Phycomycetes) as is the absence of cross walls in the order Siphonales of the green algae.

Structurally, the mycelium consists of a complicated mass of interwoven, branched filaments (Fig. 169), each of which is termed a **hypha** (plural **hyphae**). Hyphae, then, are the individual filaments or branches, and collectively the hyphae composing the vegetative stage of a given fungus plant are the **mycelium**. The medium upon which the mycelium grows is termed the **substratum**.

The hyphae, with the exception of the coenocytic condition noted above, are composed of cells, the walls of which are made up, in some cases, apparently of pure cellulose. In others, little cellulose is present, the greater part of the wall substance being a fatty-acid complex with a chitin base. Within the cells the usual cell parts are present, consisting of one or more nuclei and a mass of vacuolated cytoplasm. Sugars and glycogen, but not starch, represent the carbohydrate type of food present, but fatty

and oily materials, proteins, organic acids, and other substances also occur. Various types of pigments, but not chlorophyll, may also be present, sometimes in the cell wall and sometimes in the cell content, though typically they are absent.

Mycelium is usually abundant and easily obtained from any supply of decaying organic matter. In turning over piles of decaying leaves in late autumn or early spring, one may find it occurring as fine white strands running through them. On the lower sides of boards in damp situations, it develops rapidly (Fig. 169) or it may often be found forming large sheets or mats in the crevices of decaying logs. The presence of a reproductive body is evidence of the extensive development of mycelium in that region of the substratum. If a piece of bread or other food material rich in

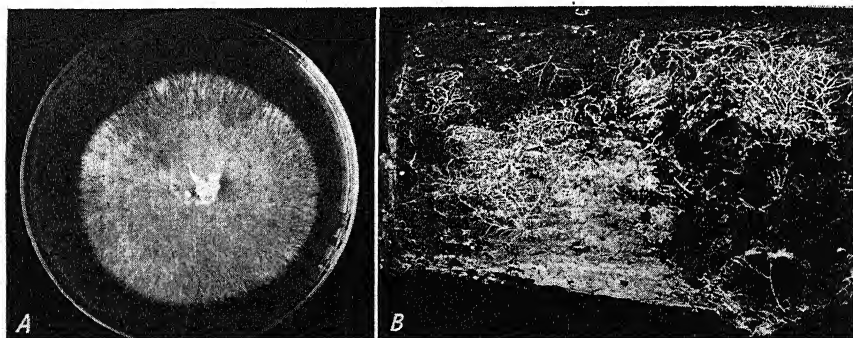


FIG. 169. A, mycelium of a fungus as grown in a petri dish in the laboratory; B, photograph of white mycelial strands on the underside of an old log in the woods.

carbohydrates is kept moist for a few days, a white cottony growth, the mycelium of a fungus, usually develops over it.

Growing in such situations as have been enumerated, the tips of the mycelium are often able to penetrate directly through the cell walls of the tissue concerned, even though it be of the hardest wood. They do this by means of enzymes, which they secrete, some of which have the power of dissolving the substances composing the cell walls. For example, the cellulose of the cell wall is ordinarily insoluble and would offer considerable resistance to mechanical penetration, but it is broken down by enzymatic hydrolysis and, moreover, yields glucose, which is assimilable by the fungus. The fungus then, in bringing about decay or disease, is only preparing, by an external digestive process, the food materials for its use. In the course of time this may result in the complete transformation of a sound log into a mass of rotten, useless material representing that portion of the tissue which the fungus is unable to use; or a perfectly sound apple, a potato, or an orange will, in the course of a few days, be reduced to a wet, rotten, pulpy

mass. In case of a mushroom or toadstool growing on a grassy lawn or in a pasture, the result of these activities is not so conspicuous, but they are continually taking place on the dead organic matter in the soil. Such activities of soil fungi, like those of soil bacteria, are important in breaking down organic matter in the soil, thereby providing materials for the growth of higher plants.

Resting Stages. In some fungi, the mycelium may pass into a dormant or resting stage by the formation of definite bodies of closely compacted hyphae known as *sclerotia*. These vary in size from half the size of a pinhead to several inches in diameter. When of sufficient size, some of them form a palatable food material for man and have been known under the names of "Indian bread," tuckahoe," and other descriptive terms. Usually, however, they are quite small or are developed within the substratum, so that they are not easily found. On the return of favorable conditions, these sclerotia may grow out into a new mycelium or they may produce a sporophore of some sort. They are more frequently found in species that are parasitic upon annual plants or plant parts. In case of parasites on the perennial parts of plants, the fungus usually hibernates as a dormant mycelium in the host tissue. In many other cases, the mycelium in its ordinary condition is, if well protected, perennial in nature.



FIG. 170. Mycorrhiza of white pine. Note that the finer rootlets, as at *a*, are abnormally swollen and show an abnormal amount of branching.

Mycorrhiza. One other mycelial relation remains to be described. It is now known that in a considerable number of cases a close relationship has been established between the mycelium of certain fungi and the roots of certain higher plants, particularly forest trees. In this association, the mycelium may form an encircling mantle around the finer rootlets or may be largely internal in the cortex of the root. Such infested rootlets are much enlarged and usually show an abnormal amount of branching (Fig. 170). This combination of fungus and host is known as a *mycorrhiza* and is a phase of those physiological relationships between organisms

grouped under the term **symbiosis**. Mycorrhizas are probably essential for the proper growth of many species of plants with which they are associated.

The Reproductive Phase. The Sporophores. The most effective method of reproduction in most fungi is by means of spores. The structure which produces these spores is called a **sporophore** and is frequently well differentiated from the purely vegetative structures. The reproductive organs are often aerial while the mycelium is usually within the substratum.

The variation in types of sporophores produced is almost endless. Some are extremely small, so minute that the naked eye cannot discern them. At the other extreme are such large sporophores as the common mushrooms or toadstools, the puffballs, and many others—structures

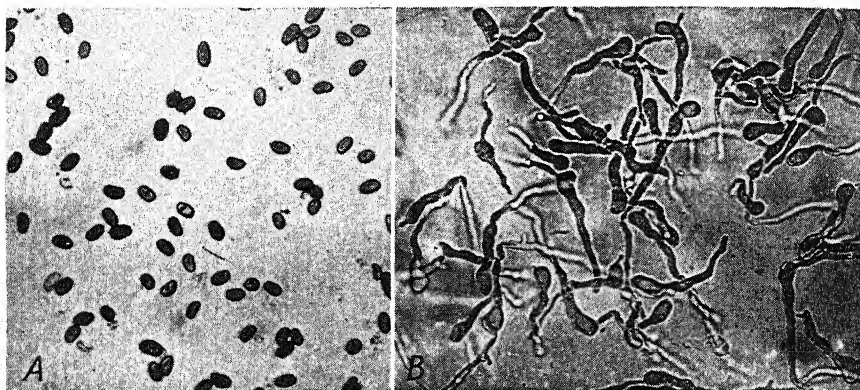


FIG. 171. Spores and spore germination. A, photomicrograph of spores of a common mushroom; B, photomicrograph of spores germinating. The bulb-like swellings are the original spore bodies.

that are usually thought of as “the fungus,” while the extensive mycelial development in the substratum is often disregarded.

The Spores. Motile spores, known as zoospores or swarm spores, are present, as would be expected, in most aquatic fungi and represent the typical asexual method of reproduction of such forms. They are formed in zoosporangia, from which they usually emerge (“swarm”) at maturity and, after a brief period of activity, germinate into a mycelium. The majority of fungi are more terrestrial in habitat and produce nonmotile, wind-disseminated spores (Fig. 171, A). These spores may be formed in any one of several different ways.

Often a given fungus may have more than one kind of spore. Usually each species has one spore type of major importance and one or more types of minor importance or for different functions. Thus many species have a spore stage in which they pass the winter, and thus the spore becomes a

resting spore. The same species may have one or more other spore forms for rapid dissemination through the growing season. It is evident that these spores, each serving a different purpose, might be quite different in structure, color, thickness of wall, and other characters. Some species of fungi are known to have as many as five different types of spores in the life cycle.

Spores in general are unicellular, but there are many instances of multicellular spores. In such cases each cell behaves as a unicellular spore, and the structure might be better regarded as a compound spore.

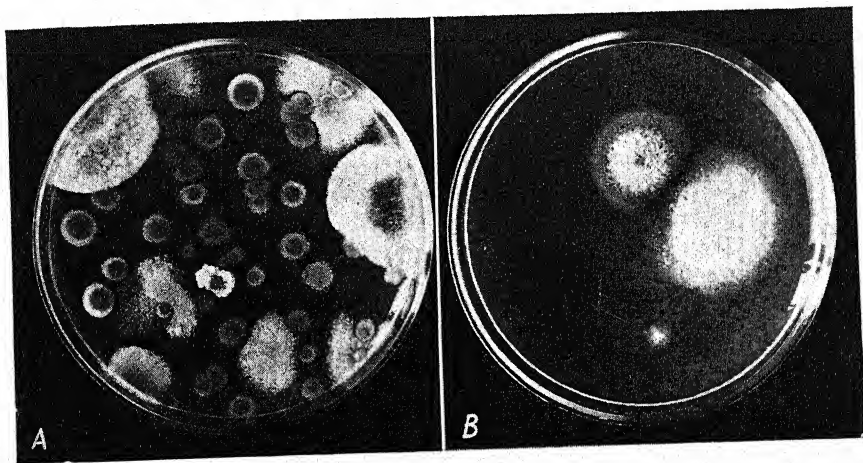


FIG. 172. *A*, dish of agar medium uncovered for 5 min. in a crowded laboratory and then incubated for 3 days. During this 5-min. interval of exposure, nearly 50 spores settled on the agar and developed into colonies. *B*, a similar dish of agar exposed for 5 min. on a stump in the woods near the laboratory, at the same time as the foregoing exposure. Only three colonies developed in the second dish.

The number of spores produced by fungi is enormous. A single mushroom sporophore is estimated to give off 40 million spores per hour during the period of active spore discharge, which covers several hours. Some other kinds of fungi, such as the large puffballs, produce many more than this. When one considers the total number of spores produced during a growing season, one ceases to wonder at the universal presence of these plants and is surprised that there are not more of them. As a result of their presence, the air about us is always more or less contaminated with spores. To prove this, one has but to uncover a dish of sterilized culture medium for a minute or two. Spores from the air settle quickly on this substratum and begin development (Fig. 172).

After dissemination, which is most frequently accomplished by wind or air currents, the spores may germinate if they meet with favorable con-

ditions. Some resting spores are so constructed that they must of necessity lie dormant for a time. An adequate moisture supply is essential to the germination process. Some spores require an actual film of water and others are able to germinate in a moist atmosphere. A correct temperature is also of great importance. In general, low temperatures as well as unusually high temperatures tend to suppress germination. The optimum for many spores is between 15 and 20°C. Spores usually germinate by extruding, through some point on the spore wall, a protoplasmic sac, which rapidly elongates into a narrow tube known as a germ tube (Fig. 171, *B*). This tube usually continues to grow and elongate and eventually becomes the mycelium. With its spores in the proper condition for germination on the proper host or substratum and with proper atmospheric conditions, a fungus may spread extremely rapidly. Such coincidences are the direct cause of the rapid and extensive spread of various plant diseases over a period of a few damp, sultry days during the growing season. Spores of many fungi can be readily germinated in tap water and are interesting objects for microscopic study (Fig. 171, *B*).

Economic Importance of Fungi. The economic importance of the different kinds of fungi is considered in connection with the discussion of the separate groups in the following pages. A few general matters may, however, be pointed out here. While many of the fungi are decidedly detrimental to man, others are beneficial and even indispensable. Some, like the mushrooms and truffles, are used as food. Others are used as sources of drugs. The yeasts are universally used in breadmaking, in the making of alcoholic beverages, and in various other fermentation processes, and are also a source of vitamins. Some fungi are used in cheese making and others in other manufacturing processes.

Soil Fungi. The importance of soil fungi is often minimized in discussions of soil fertility. From studies at the Rothamsted Experiment Station in England, it has been estimated that living fungus cell material was present in fertilized soil to the extent of 1,700 lb. per acre, which is about twice as much as the material from bacteria and all other soil microorganisms combined. These fungi are important in maintaining soil fertility not only because they break down complex organic substances such as cellulose, proteins, and other compounds, thereby transforming such substances into forms available to crop plants, but also because they utilize many inorganic substances which are thus prevented from being lost from the soil by leaching. Some of the soil fungi are more active in producing ammonia from proteins than are the ammonifying bacteria. Not all the soil fungi are beneficial, however. Some of them cause damping off of seedlings and others cause serious diseases of more mature crops. While in some cases only the spores or resting forms of these pathogens may

be present in the soil, in other cases these fungi lead a saprophytic existence in the soil, later becoming parasites.

Antibiotic Substances. Many of the fungi produce certain chemical substances which are able to inhibit the growth of or to destroy bacteria and other microorganisms. Such substances are called **antibiotics**. The best known of these substances is **penicillin**, which, since about 1941, has been widely used as a therapeutic agent against infections produced by certain bacteria, particularly those of the Gram-positive type. Penicillin is a metabolic product of the fungus, *Penicillium notatum*, from which it is produced in commercial quantities.

Another antibiotic, **streptomycin**, so named because it was originally isolated from *Streptomyces griseus*, one of the Actinomycetes, has been found to be effective against some of the bacteria that are unaffected by penicillin, particularly the Gram-negative organisms. **Aureomycin**, also obtained from one of the Actinomycetes, has been found effective in the treatment of many serious diseases of animals and man that do not respond readily to other antibiotics. Many other antibiotics have been reported from fungi and from other organisms, but many of them will probably never be used as therapeutic agents because of their toxic properties.

Diseases of Animals and Man; Medical Mycology. Many different fungi infest the bodies of animals and man. A disease caused by such infestation is called a **mycosis**. Examples of these diseases are ringworm, athlete's foot, valley fever, histoplasmosis, and aspergillosis. There are many others. Some of the fungi causing mycoses affect only the skin, while others may cause generalized infection of a more serious nature. While fatal fungous diseases in man are less common than those caused by bacteria, they are nevertheless important. According to the vital statistics of the United States, mycoses caused 284 deaths in man in 1945. In the same year, 471 deaths were caused by typhoid fever, 443 by malaria, 377 by typhus fever, 303 by scarlet fever, 185 by amoebic dysentery, 94 by undulant fever, 43 by rabies, and 12 by smallpox. The total number of deaths caused by all infections and parasitic diseases in this year was 92,933. Of these, therefore, about 3 per 1,000 were caused by fungi. It is thus seen that mycoses are more common than we ordinarily realize. They are more prevalent in tropical regions. Nonfatal mycoses are probably as common as any bacterial disease. **Medical mycology**, which is the study of the fungi causing mycoses, is rapidly becoming a prominent branch of the general study of fungi.

Plant Diseases; Plant Pathology. Diseases of plants may result from many different causes, such as mineral deficiencies or excesses; unfavorable environmental conditions of light, temperature, moisture or oxygen supply; toxic gases and other chemicals; nutritional unbalance or other internal

physiological disturbances; viruses; the attacks of eelworms, insects, mites, spiders and other animals, bacteria, actinomycetes, and fungi. Plant pathology deals with all these diseases. Of all parasitic diseases of plants, those caused by fungi are the most common. Fungi causing plant diseases are found in all the main groups of fungi, and there is hardly a plant that is not subject to the attack of one or more of them. They cause not only millions of dollars of loss annually in crop plants but many molds, mildews, and other fungi also cause spoilage of foods, destruction of fabrics, paper, and leather, and rotting of timber. It is the problem of the plant pathologist to prevent and to control such ravages. A knowledge of the fungi is therefore basic to him.

In attempts to prevent and to control diseases of plants, several methods of attack are used. Among these may be mentioned the following:

1. *Exclusion and quarantine*, by which the transportation of diseased plants from one region to another is prohibited. In 1912, the United States Congress enacted the first quarantine act for the control of plant diseases. Since then 50 or more additional Federal disease quarantines have been put into operation for preventing the spread of particular plant parasites. Almost all foreign countries as well as the individual states of the Union now have similar laws.

2. *Sanitation*, or the maintenance of sanitary conditions in the vicinity of growing plants. This involves the destruction, by burning or other means, of diseased plants or plant refuse which may harbor disease-producing organisms, or the elimination of breeding places of such organisms.

3. *Development of Resistance or Immunity to Disease*. Some varieties of plants are more resistant than others and may be wholly immune to particular pathogens. Such resistance is often a heritable character. The selection and breeding of such varieties sometimes offers the most effective or the only method of controlling certain diseases. Particularly is this true of some virus and bacterial diseases of plants, but the method has been applied to many fungous diseases as well.

4. *Selection of Disease-free Seed and Propagating Stocks*. Some diseases, like the anthracnose of beans, are carried over from crop to crop by means of diseased seed. Similarly, potato tubers and other propagating stock may harbor disease organisms. Care in the selection of disease-free seed and propagating stock may prevent the spread of certain diseases.

5. *Crop Rotation*. The spores or mycelia of some fungi are able to live over from one year to another in the soil. The length of time that such fungi can remain alive in the soil varies, but the ravages of these organisms can be reduced by not planting the same crop in the same soil year after year. In fact, one of the chief reasons for rotating crops is to reduce plant diseases.

6. *Correcting Mineral Deficiencies or Excesses in Soil.* Diseases caused by deficiencies of certain minerals in the soil often manifest themselves by yellowing, mottling, and other discolorations of leaves and other parts of plants and by reduced growth. Examples of such deficiency diseases are sand drown of tobacco caused by magnesium deficiency, heart rot of beets resulting from boron deficiency, little leaf or rosette of fruit trees caused by zinc deficiency, frenching of the leaves of various plants, sometimes caused by copper deficiency, chlorosis of spinach due to manganese deficiency, and pineapple chlorosis caused by iron deficiency. Plants also become chlorotic when there is an inadequate supply of nitrogen. In some cases these diseases are overcome by spraying the plants with salts of the deficient element and in others by applying such salts to the soil. An excess of salts of boron, zinc, copper, or other elements may also be toxic to plants. An excess of soluble nitrogen salts has frequently been reported to render plants more susceptible to infectious diseases such as fire blight, a bacterial disease of apples and pears. It is likely that there is a relationship between the relative amounts of various inorganic substances absorbed by plants and their susceptibility to invasion by parasites.

7. *Sterilization of soil or other media* by means of heat or chemicals. Partial sterilization of soils or soil pasteurization by means of electric heat or steam is a common method of disease control in greenhouses and seed-beds. It is possible to select a temperature that will inactivate many destructive organisms without impairing most of the beneficial ones or otherwise adversely affecting the soil as a growth medium. Formaldehyde and other chemicals are also sometimes used for soil sterilization.

8. *Seed treatments* by means of heat or chemicals. The object of seed treatments is to kill pathogenic organisms found in or on the seeds themselves and to prevent their invasion from the soil when the seeds are planted. The treatment may involve the use of heat. Thus a hot-water treatment is used to overcome loose smut of wheat, which is perpetuated by an internal infection of the grain. More commonly, the seeds are treated with chemicals, either in solution or as dusts. Formaldehyde or compounds of mercury, copper, or sulfur may be used. Many seedsmen thus treat their seeds before putting them on the market. Organic mercury compounds are widely used for this purpose. Some seeds, however, cannot be treated in this manner. Care must be exercised to avoid seed injury by the chemicals.

9. *Spraying or dusting of plants with fungicides* chiefly to prevent the invasion of pathogens but also to check the spread of those already present. The active ingredients of sprays and dusts are often copper or sulfur. Bordeaux mixture, which consists of lime and copper sulfate, and lime sulfur, which is a mixture of lime and sulfur, are widely used for this

purpose, although many other spray materials are now being used. Usually, an insecticide is also added to the spray material. Care must be exercised to avoid spray injury and the application of the spray or dust must be carefully timed to be effective.

10. *Eradication.* There are some "rusts" of plants that require two separate kinds of hosts to complete their life cycles. Thus the white pine blister rust has currants and gooseberries as alternate hosts. The apple rust has the red cedar as an alternate host and the black stem rust of wheat has the common barberry as an alternate host. It might be possible in a given locality to eradicate these diseases by destroying the less important host. In the case of the white pine blister rust this means that if all the currant and gooseberry plants were destroyed in a given locality, the rust might not appear on white pine because the parasite could not complete its life cycle. This method has actually proved effective in some regions. Similarly, an extensive program is now being carried out in various parts of the United States to eliminate the common barberry in an attempt to control the black stem rust of wheat. A considerable downward trend in average annual losses of wheat has been achieved by it. Naturally this method has a limited application in so far as diseases of plants in general are concerned.

Other methods besides the ones enumerated have been used in special cases, for example, the injection of chemicals into trees to overcome mineral deficiencies or to combat parasites. The use of vaccines, antitoxins, serums, and antibiotics, which are very effective in diseases of animals and man, have not met with much success with plants. This is partly because the plant pathologist must usually deal with great numbers of plants rather than with individuals and partly because plants do not have a circulatory system comparable with that of the higher animals and man. As to control measures in general, preventive measures are usually much more effective with plant diseases than are attempts to combat a disease already present.

Classification. The subdivision fungi is usually divided into the following four great classes:

Class I. Phycomycetes (Phycomyceteae), or alga-like fungi, in which spores are usually produced in sporangia, and hyphae are either lacking or, when present, are destitute of cross walls. All the following groups have septate hyphae.

Class II. Ascomycetes (Ascomyceteae), or sac fungi, in which the spores are produced in asci.

Class III. Basidiomycetes (Basidiomyceteae), or basidium fungi, in which the spores are produced, usually in fours, on a specialized structure known as a basidium.

Class IV. Fungi Imperfecti, or imperfect fungi, a group for the reception of many species, the life histories of which are not entirely known but which do not fall readily into any of the foregoing classes.

PHYCOMYCETES

General Characteristics. The class Phycomycetes includes a large assemblage of fungi that have been brought together into one group.

The vegetative plant body is either a simple protoplasmic mass or an extensive mycelium, but in neither case are internal cell walls usually formed. The plant body is, therefore, coenocytic in structure, although, in an old mycelium and during the formation of reproductive organs, cross walls may be laid down. On this character of lack of separating walls in the active vegetative mycelium, one can usually recognize a member of the Phycomycete group. Zoospores are present in those members of the group that are truly aquatic, but, in the terrestrial and epiphytic species, nonmotile wind-disseminated spores take their place in most instances. Sexuality, while present in the group, is apparently absent from the life history of some species. When present, it is isogamous in some and heterogamous in others. On this basis it is possible to divide the group into the two subgroups, *Zygomycetes* and *Oömycetes*, the former isogamous, the latter heterogamous.

Of the seven orders of Phycomycetes usually recognized, we can consider here but three, as follows:

Order I. Saprolegniales. Filamentous, phycomycetous fungi with heterogamous sexual reproduction; parasitic or saprophytic water molds. This and the order Peronosporales make up the major part of the subgroup *Oömycetes*.

Order II. Mucorales. Filamentous, phycomycetous fungi with isogamous sexual reproduction, if any; mostly saprophytic; comprises most of the subgroup *Zygomycetes*.

Order III. Peronosporales. Filamentous, phycomycetous fungi with heterogamous sexual reproduction, if any; parasitic on higher plants.

Order I. Saprolegniales. This is an order composed almost entirely of aquatic fungi living as saprophytes on various forms of decaying organic matter or more rarely as parasites, particularly of animal life. They are easily grown in the laboratory by placing the bodies of dead insects or pieces of fresh meat in stagnant water for several days. Some species are abundant in soil. A small amount of top soil placed in stagnant water with a small piece of fresh meat or boiled flaxseed often yields an abundant growth of the fungus. Correlated with the aquatic habitat, zoospores produced in zoosporangia form the means of asexual reproduction. A high type of heterogamous sexual reproduction is also present, comparable

with that found in the higher filamentous algae. The order is a comparatively small one, including about 16 genera and about 100 species.

The Mycelium. The mycelium usually develops in profusion, forming a white mold-like growth over the substratum. In addition, there is always a well-developed mycelium within the substratum. There is little differentiation between the mycelium of these plants and that of any other group of the Phycomycetes. The cell wall is said to differ in composition from that of practically all other fungi, giving a reaction for true plant cellulose. Cross walls are absent or very sparingly present and the many minute nuclei are contained in a body of highly vacuolated cytoplasm that is quite colorless and often very granular. The filaments composing the mycelium increase rapidly in length by apical growth.

Asexual Reproduction. Asexual reproduction is accomplished through the formation of zoospores in zoosporangia. These zoosporangia are usually club-shaped and are formed at the tips of the hyphae, or less often they are more globose and formed at intervals along the filament. In either case, the young sporangium contains a multinucleate protoplasm and is cut off by a wall from the rest of the filament (Fig. 173, A-C). The protoplasm usually does not completely fill the sporangium but forms a parietal layer, the center of the sporangium being occupied by a large vacuole. Irregular clefts or furrows then appear in the protoplasm, beginning at the vacuole and extending outward. When these furrows are completed, the protoplast has been divided into numerous uninucleate bodies, each of which becomes a zoospore (Fig. 173, C). In other cases, the undivided protoplast is discharged from the sporangium as a naked mass that invests itself with a membrane, and the protoplasm then divides to form the zoospores. The escape of the zoospores is termed "swarming." When they first emerge from the sporangium, they are pear-shaped and are provided with two terminal cilia. Often, after a few minutes of activity, they go into a resting stage. When they emerge from this, after several hours, they are kidney-shaped and laterally biciliate. These two types of swarming were formerly regarded as generic attributes, but recent work tends to show that in the same species they may swarm but once or they may swarm twice. The zoospores germinate by producing a germ tube that grows out to form a mycelium.

In several genera, and probably under special environmental conditions, the protoplasmic content of the sporangia becomes cut up into spore-like bodies. Since these never produce cilia and do not escape from the sporangium, they can hardly be regarded as true zoospores. These bodies germinate in place, each producing a coenocytic germ tube that grows out through the sporangial wall (Fig. 173, D).

In some species, asexual reproduction takes place by the formation

of **gemmae**, in which a filament becomes divided into short cells that swell into ellipsoid or globose form (Fig. 173, *E*, *F*). After a short rest period, each of these may germinate by producing a germ tube that grows into a mycelium.

Sexual Reproduction. Much work has been done on the problem of the sexuality of the Saprolegniales, but the results have been very conflicting and general conclusions must be drawn with caution. In some species

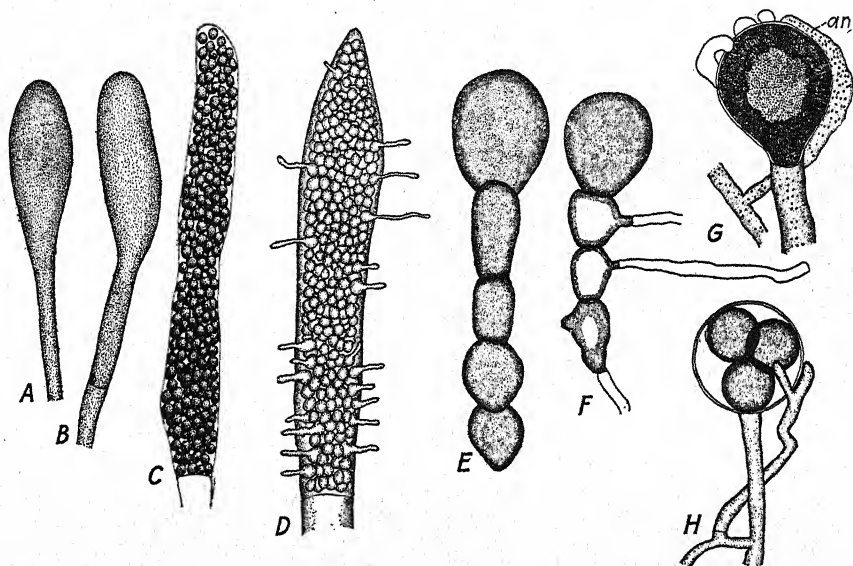


FIG. 173. *A-C*, *Saprolegnia ferax*. *A* and *B*, young zoosporangia forming at the tips of hyphae and becoming dense with cytoplasm; the sporangium is then cut off from the rest of the hypha by a cross wall, as in *B*; *C*, mature sporangium packed with zoospores ready to emerge; *D-F*, asexual reproduction in Saprolegniales; *D*, tip of filament containing zoospore-like bodies, some of which have germinated, the germ tubes penetrating the hyphal wall; *E*, *F*, formation of gemmae and their germination into hyphae, in a species of *Pythiopsis*; *G*, *H*, sexual reproduction in Saprolegniales; *G*, a pear-shaped oogonium of a species of *Saprolegnia*, to which are attached four antheridia, *an*; *H*, a mature oogonium of a species of *Achlya*, containing three eggs, with a fertilization tube penetrating the oogonial cavity. (*A-C*, drawn by Chris. Hildebrandt; *D-H*, drawn by Edna S. Fox.)

oögonia are produced in profusion, but antheridia are never formed; yet the eggs develop into zygote-like structures that germinate just as if formed by a normal fertilization process. Such a development is termed **parthenogenesis**. In other species, antheridia are present, but whether or not they function has not been definitely proved. Where a functional sexuality is known to exist, it is always a high grade of heterogamy with well-developed oögonia and antheridia.

The oögonia are usually produced terminally on a main filament or a lateral branch. They originate as globular swellings into which flows the

protoplasm from the terminal part of the hypha. Then the oögonium is cut off from the rest of the filament by a transverse wall (Fig. 173, G, H). All but one of the numerous nuclei in the oögonium degenerate and disappear, or in some genera several may remain. Those that remain become the nuclei of the one or more eggs that are produced in the oögonium.

While the oögonium is developing, the antheridium appears, usually as a short, club-like branch from the hypha below the oögonium or sometimes from another hypha. The young antheridium contains several nuclei and is separated from its filament by a basal wall (Fig. 173, G, H). It grows upward until it comes in contact with the oögonium, whereupon the antheridium puts out a small lateral tube known as a fertilization tube, which pierces the wall of the oögonium. In case the oögonium contains several eggs, this tube branches and sends a branch to each of them. The tip of the tube, or its branches, comes in contact with the egg and some authors describe subsequently a true fertilization by one of the male nuclei. Others are just as confident that, at least in some species, no transfer of the male nuclei ever takes place and that further development is parthenogenetic.

Regardless of whether the development is parthenogenetic or follows fertilization, the cell walls of the eggs gradually become thickened and dark colored. Usually after several months of dormancy they germinate by producing a germ tube which may very soon develop a zoosporangium with zoospores.

Economic Importance. The members of this order nearly all live saprophytically. One or more species of *Saprolegnia* are believed to cause a serious disease of fishes, and the disease may assume serious proportions at times in fish hatcheries and in aquaria. The diseased individuals become sluggish in their activities and, in the later stages, a white or grayish mold-like growth appears over the surface of the body, making its first appearance usually in the region of the gills. The host soon dies, but the numerous zoospores formed by the fungus quickly spread the disease to other individuals or to the eggs and can be eliminated only by thorough disinfection of all vessels and troughs used. Great care should always be exercised in handling living fish, as it is believed that even the rubbing off of the slimy material that normally coats the external body of the fish will facilitate entrance of the parasite, while bruises and wounds should be especially avoided. Members of this same genus, and others as well, are often found growing in abundance on dead fish, on amphibians, such as frogs, and on turtles along streams, but this is no certain indication of the parasitism of the fungus in every instance. In fact, some maintain that these fungi are incapable of infecting fish that are entirely healthy but that only sluggish or diseased individuals can be successfully attacked.

Summary of Saprolegniales. The Saprolegniales are aquatic fungi inhabiting dead organic material or perhaps occasionally growing parasitically. As in most other Phycomycetes, the mycelium is well developed and coenocytic in structure. Correlated with the aquatic habitat is the production of zoospores in zoosporangia, the zoospores often going into a resting stage and swarming a second time with a corresponding change in body shape and in the position of the cilia. Oögonia and antheridia are present and functional in some species. In others, these organs may be present, but the antheridia may not function. In still others, antheridia

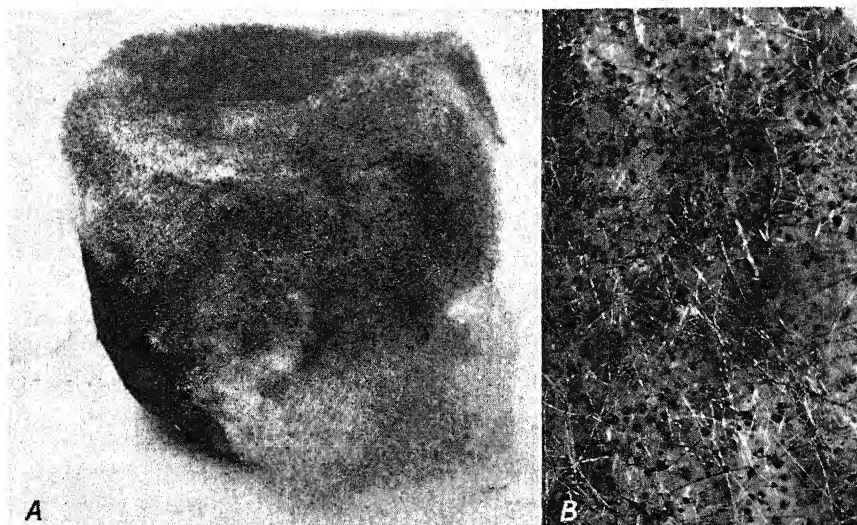


FIG. 174. A common black mold, *Rhizopus nigricans*. A, half a loaf of bread kept in a moist container for several days; the cottony growth is the mycelium; the minute dots are sporangia; B, photograph somewhat enlarged, to show the black sporangia.

are not formed, and development from the egg is parthenogenetic. Typically the zygotes require a long period of dormancy before germination.

Order II. Mucorales. This order contains about 150 species, some of which are familiarly known as "black molds." They are mostly saprophytic fungi and are extremely abundant on decaying organic matter, particularly if it is rich in starches and sugars. Some species are parasitic on other fungi. The black color characteristic of the mature stage of many species is due to the asexual spores produced in that stage. The vegetative portion (mycelium) of the plant body is colorless or slightly brownish and is usually produced in profusion on the substratum. Spores of these fungi are always in the air. In order to obtain a luxuriant growth of these molds, it is only necessary to expose a piece of bread or similar materials in a damp atmosphere for a few days (Fig. 174, A). *Rhizopus*

nigricans is a common species easily developed in this way. From the preceding order, the Mucorales differ chiefly in the more terrestrial habitat, the absence of zoospores in the life history, and the presence of a special type of sexual reproduction known as conjugation.

The Mycelium. The mycelium of these fungi is always well developed and usually covers the substratum with a thick mold-like growth of tangled hyphae. A portion of it is embedded in the substratum, but much of it is superficial. At intervals on the superficial hyphae, root-like projections known as **rhizoids** are developed in a few species. These rhizoids penetrate the substratum and serve as anchors for the superficial mycelium. This mycelium consists of branched, nonseptate filaments which contain abundant cytoplasm with numerous minute nuclei. Cytoplasmic streaming is often observed in these hyphae. While a nonseptate condition is characteristic of the young, vigorously growing mycelium, cross walls are frequently found in the older hyphae, and the reproductive parts are generally separated by septa from the vegetative portions.

Asexual Reproduction. Asexual reproduction (Fig. 175, *E-I*) is accomplished by the formation of nonmotile, wind-disseminated spores. Usually they are produced in sporangia formed at the apex of erect hyphae, termed **sporangiophores**. The sporangia are visible as small, round black bodies on the mycelium (Fig. 174, *B*). In the formation of these sporangia the tip of the hypha begins to enlarge and into this enlargement a certain amount of protoplasm flows from the adjoining region. Further enlargement results in a globose terminal swelling filled with multinucleate protoplasm. This protoplasm eventually becomes transformed into spores. In many genera there is a progressive cleavage of the sporangial protoplasm from outside to center, or vice versa, with the result that the protoplasm becomes cut up into irregular, multinucleate blocks. In some cases, these blocks are of large size after the first cleavage, and later their size is further reduced by other divisions. Eventually, these ultimate units take on a definite wall and become the spores, which are in most cases uninucleate. Early in this cleavage process, a dome-shaped area of vacuoles appears within the sporangium and connects at its base with the base of the sporangial wall. These vacuoles fuse into one continuous cavity bounded above and below by a plasma membrane. At the surface of the lower of these two membranes, a wall is laid down which effectively separates the developing spore mass from the dome-shaped region known as the **columella**. The columella, therefore, projects up into the cavity of the sporangium. When the sporangial wall breaks and releases the spores, the columella remains as a conspicuous structure on the old sporangiophore. In some species a columella is not present.

In general, the sporangia are globose or pear-shaped, and but a single one

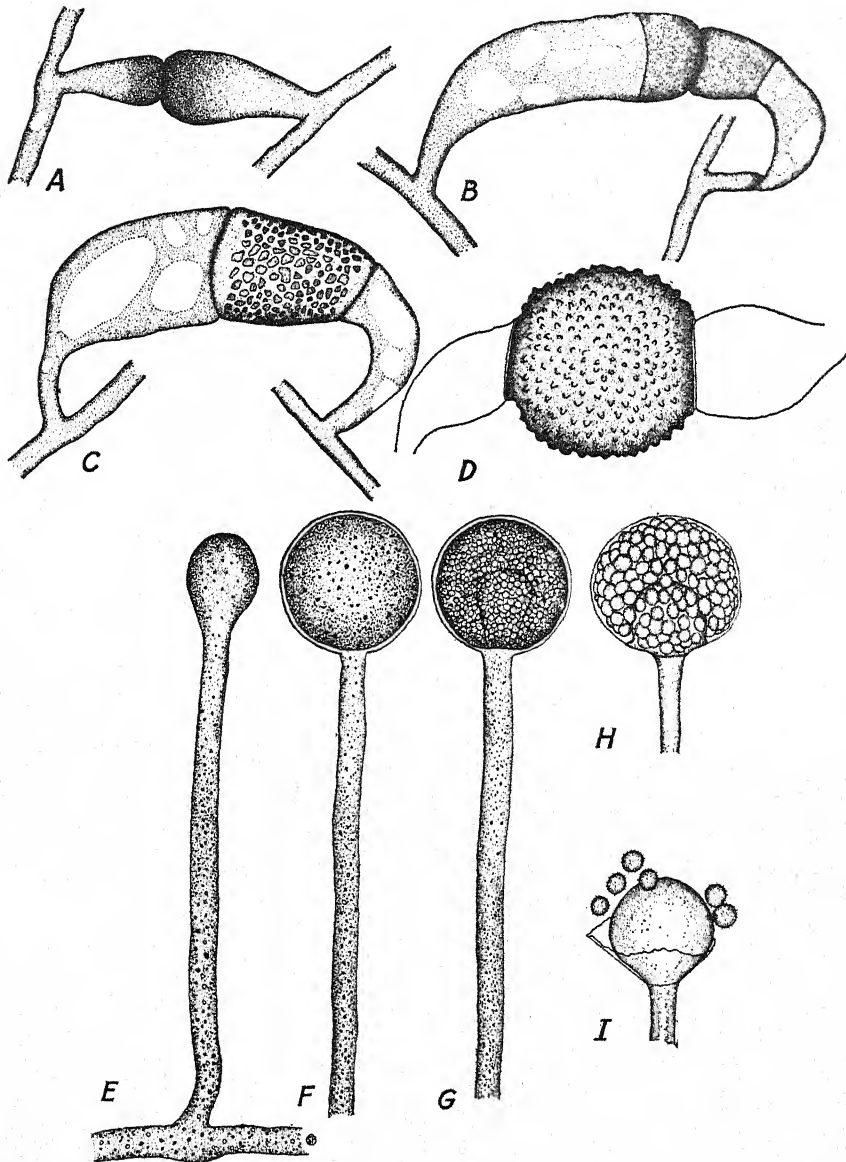


FIG. 175. A-D, stages in the sexual reproduction of a black mold. A, two lateral hyphal branches in contact, the protoplasm accumulating in the ends of each branch; B, tip of each branch cut off by a cross wall, two gametangia in contact; C, coalescence of the two gametangia has occurred and pads of thickening are beginning to appear on the wall of the young zygo-spore; D, mature zygospore with black, warted wall; E-I, sporangium development in a black mold; E, hyphal tip enlarging to form a sporangium; F, sporangium before spore formation; G, sporangium with spores cut out and columella visible; H, sporangium with mature spores and a distinct columella; I, sporangium with wall broken, leaving a ragged fringe at the base of the globose columella. (Drawings by Ernest Geisweide.)

is produced on each sporangiophore or stalk. Occasionally, however, the sporangiophore branches and bears several sporangia. Sometimes the sporangia are described as cylindrical tubes produced several on the head of a sporangiophore, each containing a single row of spores. In such species, the wall of the sporangium is extremely evanescent, and the whole structure is likely to be interpreted as a series of chains of spores. The spores in many species become dark-colored at maturity and possess various sculpturings or other markings on the exterior wall. All of these sporangiospores are nonmotile. They germinate into new filaments or mycelia.

Sexual Reproduction. Sexual reproduction of the conjugation type is characteristic of the Mucorales (Fig. 175, A-D) and is surprisingly uniform. Its sequence in *Rhizopus nigricans* may serve to illustrate the whole group. Where two hyphae lie in proximity, a short club-like branch, rich in protoplasm and multinucleate, is put out from each. These meet end to end in most genera, but at a very acute angle in others. In some species these protuberances are of the same size; in others one is considerably larger than the other. Gradually the two filaments are pushed apart by the growth of these protuberances. The tips of these branches become densely packed with protoplasm and a wall is formed in each, cutting off the extreme tip from the remainder of the branch. The cells so cut off are regarded as multinucleate gametangia and sometimes contain as many as a thousand gamete nuclei. The remainder of the special branch bearing the gametangium is known as a **suspensor**. The double wall between the two gametangia is broken down and the protoplasm of the two gametangia mingles. Most investigators describe a subsequent fusion of nuclei in pairs, and apparently one gametangium usually carries a larger number of nuclei than the other, for there usually appear to be several nuclei left over which do not fuse and which later disintegrate. Others find evidence which indicates that in other species the number of nuclear fusions is reduced. Sometimes only two or four pairs of nuclei fuse, all other nuclei degenerating. The resulting zygospore increases in size and forms a heavy, dark, and often spiny or otherwise roughened wall. The germination of these zygospores has not been followed in many genera. In *Mucor* and *Rhizopus*, after a considerable rest period, each produces short hyphae, on the tips of which arise new sporangia known as germ sporangia, producing nonmotile spores. In other genera, the zygospore develops directly into a new mycelium.

Sexual reproduction is now known to occur in most Mucorales but in some genera it is rarely observed. The reason for this was discovered by Blakeslee in 1903. He found that in this order (and his observations have since been extended to other groups of the fungi) the species are

separable into two distinct types that he has designated **homothallic** types and **heterothallic** types. In the former, conjugation will take place between the hyphae originating from a single spore; *i.e.*, two hyphae from the same mycelium may conjugate. Consequently, zygospores are not difficult to find in homothallic species. In heterothallic species, conjugation is dependent upon the presence of mycelia which have arisen from two inherently different spores. These two types of mycelia are regarded as different sexual strains of the fungus and sometimes are actually different enough to be easily recognized by macroscopic examination. They have been designated as "plus" strains and "minus" strains. The plus strain often shows somewhat more vigorous growth than the minus strain, and the gametangia are sometimes of correlated size. If several spores of each of these strains are "planted" at different places on a nutrient substratum and allowed to grow until their mycelia meet, conjugation will take place between the hyphae of the two different strains, and zygospores will be formed in abundance along the line of union of plus colonies with minus colonies. Where the mycelia from two plus colonies or two minus colonies coalesce, no sexual reproduction will take place. These facts explain the variable results obtained in attempting to secure material illustrating sexual reproduction by simply incubating a proper unsterilized substratum, as, for example, a piece of bread. If a spore from a homothallic species is present, or both a plus and a minus spore of the same species, conjugation will occur and zygospores will be formed. More often only plus spores or only minus spores, but not both, will be present. The mycelia will, therefore, all be alike, and no zygospores will be obtained.

Of further interest is Blakeslee's observation that a strictly homothallic species will always produce, in the germ sporangium, spores that are alike, *i.e.*, spores that will always produce homothallic mycelia. In some heterothallic species, however, the germ sporangium will contain either all plus spores or all minus spores. Therefore, in order to obtain mycelia that will conjugate, it is necessary to have spores from two different germ sporangia. In other heterothallic species, the germ sporangium contains both plus spores and minus spores.

It sometimes happens that, for some reason, the process of conjugation is arrested after the gametangia form but before fusion takes place. In such instances, the gametangia round off, form thick walls, and are termed **azygospores**. The germination of the azygospores has not been carefully studied, but in *Sporodinia grandis* they have been observed to produce a scanty mycelium that soon died.

Summary of the Mucorales. The Mucorales form a rather heterogeneous order of fungi in which the absence of zoospores and the presence of conjugation as a sexual process are the outstanding characters. Asexual reproduction is usually limited to nonmotile spores, sporangiospores,

produced in definite sporangia. The dissemination of these spores by the wind is correlated with the more terrestrial or aerial habitat. Conjugation occurring between branches of the same plant in homothallic species, and between branches of different plants (plus and minus) in heterothallic species, results in the formation of a thick-walled zygospore that, in some species, produces a germ sporangium and, in others, a mycelium. Azygospores are sometimes formed.

Order III. Peronosporales. In the order Peronosporales is included a small group of probably about 300 species of fungi, most of which are parasitic in the tissues of higher plants. In most respects they show the highest development of all Phycomycetes in that they (1) are terrestrial in habit, (2) have developed an air-borne type of spore, and (3) have a high-grade heterogamous sexual reproduction.

The Mycelium. In all species there is present a well-developed mycelium composed of coenocytic hyphae or with only occasional cross walls. This mycelium is located in the tissues of the host, usually completely filling the intercellular spaces or occasionally penetrating to and developing profusely within the cell cavity. This mycelium is usually of more regular form and of smaller diameter than the mycelium of the aquatic Saprolegniales. Haustoria are usually present. In many of the species, a parasitic mode of existence is so essential to the fungus that no one has ever succeeded in growing them out of contact with a living host. In contrast to the preceding order, there is here developed little or no mycelium external to the substratum, but in some cases, after the death of the host, the mycelium becomes somewhat external on the decaying portions.

Asexual Reproduction. Asexual reproduction is usually accomplished through the formation of wind-disseminated spores that are termed **conidia**. In one genus (*Albugo*), extremely common as a parasite on many hosts belonging to the mustard family, these bodies are cut off in chains from the tips of special hyphae, known as **conidiophores**, that are grouped in white blister-like patches under the epidermis of the host (Fig. 176, A). The fungus has been called a "white rust" on this account. When the conidia approach maturity, they burst through the epidermis and are disseminated. In most other genera, these bodies are produced on erect, aerial, simple or branched hyphal stalks that arise from the internal mycelium, frequently emerging to the outside by way of the stomata of the host plant and, under a microscope, often presenting the appearance of plums hanging on a branched twig (Fig. 176, B-D). In nearly all cases the conidia are deciduous, like spores, and in some genera they germinate by means of a germ tube as spores normally do. In others they germinate by producing a number of kidney-shaped zoospores, each with two lateral cilia, and so are sometimes termed zoosporangia

although, in the taxonomic literature, the term conidia is usually applied to them. In either case, they serve effectively to propagate the fungus.

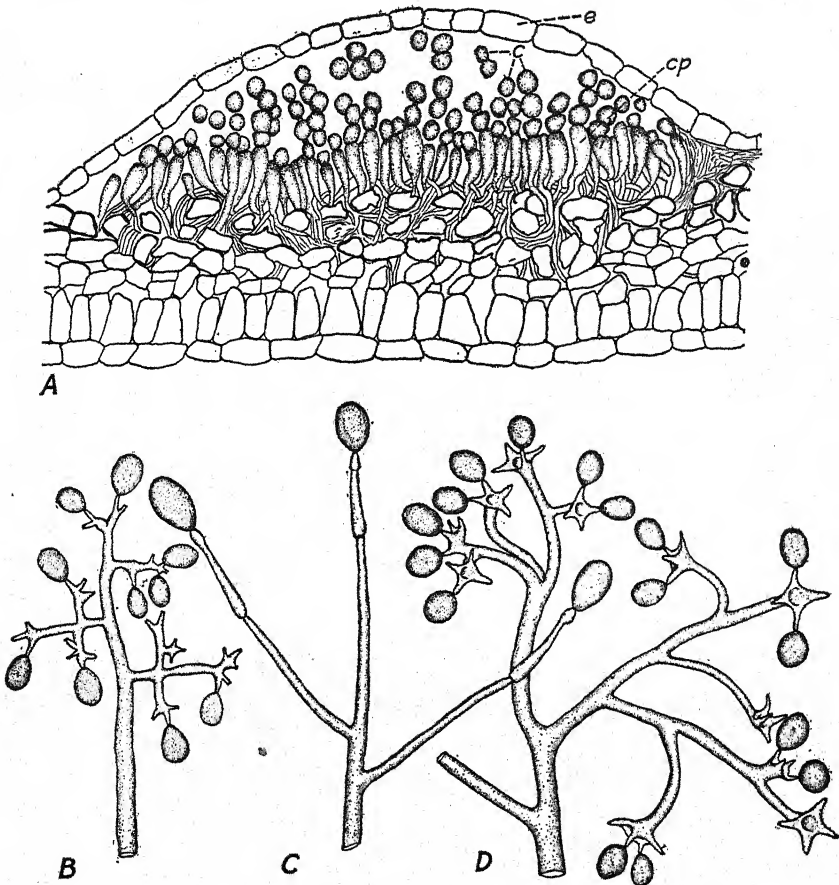


FIG. 176. Asexual reproduction in Peronosporales. A, section through a leaf of shepherd's-purse bearing a conidial pustule of *Albugo candida*; the conidia, c, are formed in chains from a basal palisade layer of club-shaped conidiophores, cp; the pustule is covered by the leaf epidermis, e; B, conidiophore and conidia of the fungus (*Plasmopara viticola*) causing the downy mildew disease of grapes; C, conidiophore and conidium of the fungus (*Phytophthora infestans*) causing the late blight of potatoes; D, conidiophore and conidia of the fungus (*Bremia Lactucae*) causing the downy mildew of lettuce; the conidiophores in B, C, and D are exserted through the stomata on the lower leaf surface. (A, drawn by Edna S. Fox; B-D, by Ernest Geisweite.)

The germ tube of the conidium or of the zoospore may, under suitable conditions, enter the body of the host plant and, by the production of a mycelium, set up an infection within its tissues. Under more unfavorable conditions, it has been reported that these zoospores, in some genera, may

encyst and then swarm a second time, as in the order Saprolegniales, but with this difference, that the second spore is just like the first one, only perhaps somewhat smaller. If the zoospores are prevented from leaving the sporangium they may, after a brief period of encystment, germinate *in situ*. The germ tube thus formed penetrates the sporangial wall and becomes a short sporangiophore, bearing at its tip a very small sporangium that contains a single zoospore.

Where these conidia (zoosporangia) are being produced abundantly, the surface of the host may present a white powdery or cottony appearance. On this account, these fungi are popularly known as the "downy mildews." The conidia furnish the chief means of reproduction in some genera.

Sexual Reproduction. All members of the order Peronosporales have a heterogamous type of sexual reproduction. Oögonia and antheridia are

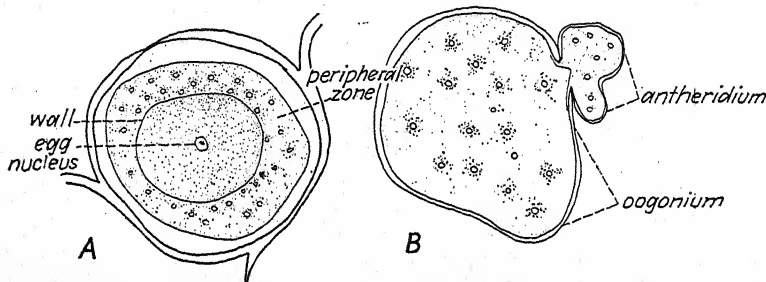


FIG. 177. Sexual reproduction in *Albugo*. A, section through an oögonium in which the single central egg nucleus has just been fertilized and a wall is forming about the oöspore, separating that body from a peripheral zone of cytoplasm containing degenerating nuclei; B, section through an oögonium and an antheridium, each with numerous nuclei.

formed much as in the order Saprolegniales. The oögonia arise as globose swellings on the hyphae in the intercellular spaces of the host plants. They are cut off from the rest of the hypha by a basal wall. The antheridia usually arise near the bases of the oögonia as short, lateral, club-shaped branches which curve up and over that organ. Both of these structures are at first multinucleate (Fig. 177). In nearly all species all but one of the nuclei in the oögonium disintegrate and this one becomes the nucleus of the single egg that is always matured. The tip of the antheridium comes into contact with the tip of the oögonium, and a passageway is dissolved between the two. A fertilization tube enters the oögonium as in the Saprolegniales, and a single male nucleus passes into the oögonium and fuses with the egg nucleus. In one or more species (*Albugo Bliti*), the oögonium is a multinucleate structure, and a number of male nuclei are discharged into it, resulting in a fusion of nuclei in pairs. The resulting zygote (oöspore) becomes a heavy-walled resting body that persists within the tissues of the host plant over winter. In the spring, the decay and

disintegration of the host tissue set the oöspores free, and under favorable conditions they germinate, in some genera forming a mycelium, in others giving rise to zoospores.

Contrary to the condition found in the Saprolegniales, parthenogenesis, if it occurs here, is unusual, a functional sexuality having been found in most species investigated.

Economic Importance. Of all the Phycomycetes, this order is of the greatest economic importance, since it contains so large a proportion of species that are parasitic on higher plants.

The downy mildew of the grape is a very important disease caused by one of these fungi, *Plasmopara viticola*. It was noted in America as early as 1834 and has since been introduced into Europe, where it has become extremely destructive in the vineyards of southern Europe. It was in connection with the control of this disease that the fungicidal properties of Bordeaux mixture were discovered. This substance, used as a spray, will effectively control the disease.

By far the most important of these fungi is *Phytophthora infestans*, the cause of "late blight" of the potato plant. Under favorable atmospheric conditions for the growth and dissemination of the fungus, it becomes one of the most destructive of all plant parasites. In 1845, there occurred in Ireland a serious famine due to the ravages of this disease. The fungus attacks the leaves, stems, and tubers of the potato plant and in severe cases the entire plant above ground is killed. On the lower surfaces of the diseased leaves there appears a white moldy growth comprising the conidiophores and conidia of the fungus. The tubers produced by diseased plants are likely to rot in the soil or later in storage. Fortunately this disease can be controlled by thorough spraying with Bordeaux mixture, beginning soon after the plants come through the ground and continuing at intervals of 10 days during the entire growing season. This fungus also causes tomato blight, which in recent years has caused serious losses to tomato growers.

A serious disease of seedling plants of many kinds, in greenhouses and in nurseries, is often caused by species of *Pythium*. The plants are attacked near the ground line, the tissues killed and rotted so that the plants fall over. The disease is known as "damping off." It may be partly prevented by lowering the humidity of the atmosphere and by using a more porous or sterile soil in which to grow the plants.

Summary of the Peronosporales. In the Peronosporales the coenocytic character of the extensively developed mycelium is in close agreement with that of the previously described orders of the Phycomycetes. They differ in habitat, the members being characteristically parasitic in the tissues of seed plants. Asexual reproduction is by a type of spore known

as a conidium that is wind disseminated and may germinate either by producing a germ tube or by producing zoospores. These spores have not been able to disassociate themselves entirely from a water habitat, and this points to a relationship with some of the preceding orders. Sexual reproduction is heterogamous and parthenogenesis occurs rarely, if at all. Several species are of great economic importance because of their ability to produce serious diseases of important crop plants.

ASCOMYCETES

General Morphology. *Limits and General Characteristics.* The group Ascomycetes includes a total of about 40,000 species, almost half of the entire number of fungi. They have little in common with the preceding group (Phycomycetes) but show considerable uniformity among themselves. They are extremely common at all seasons of the year but in general are quite inconspicuous, since often the entire plant develops entirely within the substratum, particularly in wood- or plant-inhabiting species. It is all but impossible to pick up a meter-length dead stick in the woods without finding one or more species of Ascomycetes inhabiting it. Many are terrestrial. Such species produce fruiting bodies that are fleshy in texture and may reach considerable size, sometimes weighing a pound or more. Most of the species are saprophytes, but there are many parasitic species, some of considerable economic importance.

Notwithstanding these diversities in form, they present certain uniformities of structure and reproduction that make the group quite a homogeneous one. The mycelium is always septate and there are always present in the life history spores known as **ascospores**, produced in sacs known as **asci** (singular **ascus**). The number of spores produced in each ascus is rather constantly eight, although there are exceptions to this.

The plant body, except in a single group of species that includes the yeasts, consists of a mycelium, together with some sort of reproductive structure involving one or more asci and their contained spores. In addition, the life history may be complicated by the presence of certain additional fruiting (spore-producing) stages to be described later. The spores formed in these stages are known as **conidia**.

The Mycelium. The mycelium of Ascomycete fungi is usually developed within the substratum; in a few cases only is the bulk of it superficial. In saprophytic species, it undoubtedly is quite extensive, but in many parasitic species it is restricted to a region in the immediate vicinity of the point of infection. Sometimes it is entirely intercellular, but very frequently special hyphal branches penetrate the living cells and then enlarge or become branched to form special absorbing organs known as **haustoria**. The mycelial filaments are divided by septa into uni- or

multinucleate cells. In this character is shown a distinct contrast to the mycelium of most Phycomycetes. Branching is extensive, particularly in the internal mycelium.

The Asci. The most characteristic and uniform structure in the Ascomycetes is the ascus. In many species it is a product of a sexual fusion and so has earned for that stage of the fungus the title of the **perfect stage**. Even where the sexual act is abortive or entirely suppressed, the term retains its significance as the stage in which ascospores are produced. Typically, the asci are cylindric in shape and the spores are produced in one or two rows in them (Fig. 178, *E*, *F*). Less frequently they are

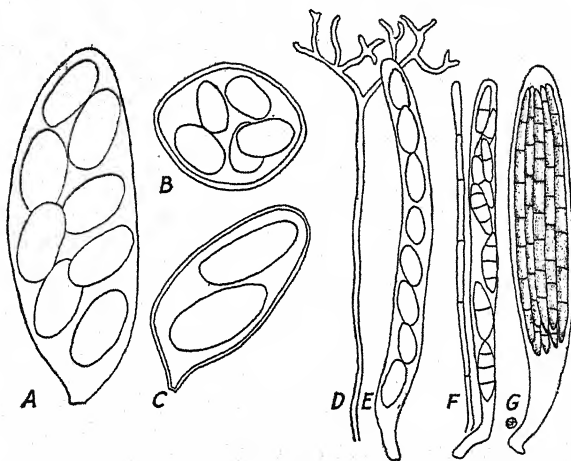


FIG. 178. Asci, paraphyses, spores, and spore arrangements in Ascomycetes. *A-C*, broader types of asci; *A* with eight spores; *B* with five; and *C* with two spores in *Physalospora*, *Podosphaera*, and *Phyllactinia*, respectively; *D*, antlered paraphyses of *Propolis faginea*; *E*, eight-spored cylindrical ascus of *Propolis faginea* with spores in one row; *F*, cylindrical ascus and a cylindrical septate paraphysis of *Leotia stipitata* with spores two- to four-celled; *G*, ascus of *Ophiobolus fulgidus* with eight elongate several-celled spores. (Drawn by Edna S. Fox.)

more or less globose and the spores without definite arrangement (Fig. 178, *B*). Often these asci are arranged side by side in a definite layer (Fig. 179, *B*), termed the **hymenium**. But sometimes the asci stand singly (Fig. 178, *A*) or show an irregularity of arrangement and no definite hymenium is formed.

In some of the simpler Ascomycetes, as the yeasts, the entire plant (cell) becomes transformed into an ascus. More frequently, the asci arise as terminal or subterminal cells of special hyphae, called **ascogenous hyphae**, which often originate as outgrowths from an oögonium and are the early products of a sexual process. The cell of the ascogenous hypha from which the ascus arises is binucleate (Fig. 180, *A-C*), one nucleus

having come from a male parentage and the other from a female parentage or their equivalents. Into the short tubular outgrowth usually developed from this parent cell, the two nuclei migrate and fuse (Fig. 180, *D*). The fusion nucleus then divides into two, these two into four, and the four into eight nuclei (Fig. 180, *E-G*). One of these divisions is a reduction division. Each of the eight nuclei, with a considerable amount of surrounding cytoplasm, is then cut out as a spore. Usually a certain amount of cytoplasm is left over in the ascus after the spores are cut out; this is known as **epiplasm**.

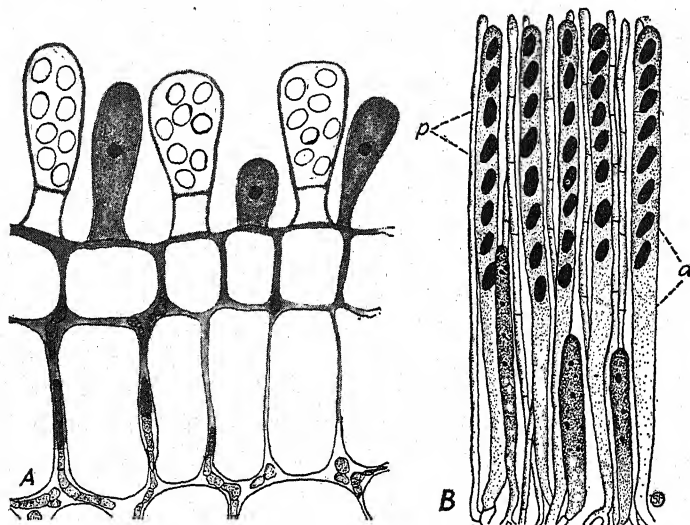


FIG. 179. *A*, three mature asci of *Taphrina deformans*, the peachleaf curl fungus, protruding singly from the epidermal cells of the leaf, each ascus with eight small spherical spores; the three darker structures are immature asci; *B*, asci and paraphyses of *Peziza* standing closely united to form a hymenial surface, each ascus with eight spores; *a*, ascus, *p*, paraphysis. (*B* drawn by Edna S. Fox.)

Sometimes some of the eight nuclei degenerate without forming spores or sometimes only two divisions occur in the young ascus, in which case the number of spores produced is less than eight. In other cases the original eight nuclei or eight spores divide and a larger number is formed, these numbers usually being multiples of 8, as 16, 32, or 64. The spores are usually unicellular, but some are multicellular with cross partitions only (Fig. 178, *F-G*), and others have both crosswise and lengthwise partitions. In all cases each cell behaves as a separate unit, germinating as a single-celled spore; hence multicellular spores are really compound spores.

The Paraphyses. Interspersed between the asci of a well-developed

hymenial layer, there frequently occur sterile thread-like bodies, usually slightly exceeding the asci in length and only a fraction as wide (Figs. 178, *D*, *F*; 179, *B*). These are termed **paraphyses**. The only function usually attributed to these structures is that of protection for the asci, especially from external contacts—perhaps also from other agencies. The possibility of their being protective in function is emphasized by the fact that their tips are often agglutinated together to form a compact membrane known as an **epithecium**. In a few cases, they seem to be nutritive in function, being consumed and disappearing as the asci mature.

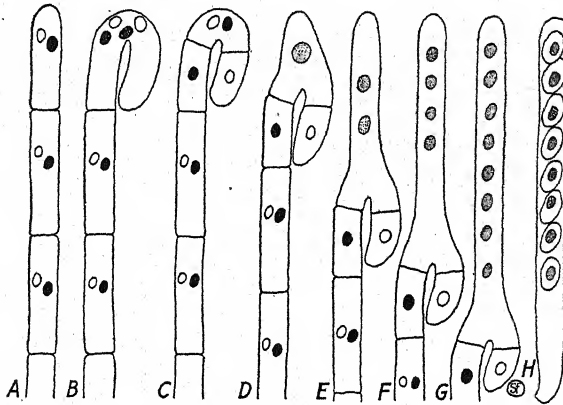


FIG. 180. Diagrammatic representation of the usual mode of ascus formation. *A*, an ascogenous hypha with binucleate cells, the nuclei shown unlike to indicate their probable sex difference; the tip of such an ascogenous hypha turns over to form the apical crook illustrated in *B*; the two nuclei of this ascus hook divide, forming four nuclei, as in *B*; transverse walls are laid down in this hook, forming a uninucleate terminal cell, a binucleate penultimate cell, and a uninucleate antepenultimate cell as in *C*; the two nuclei in the dome cell fuse and that cell begins to elongate upward, as in *D*; as it elongates, a series of three nuclear divisions results in the appearance of eight nuclei, as in *E*, *F*, and *G*; walls are laid down cutting out the eight spores as in *H*. (Drawn by Edna S. Fox.)

Fruiting Structures. *The Perfect Stage.* The fruiting body representing the perfect stage of an Ascomycete is generally known as an **ascocarp**. The simpler types of Ascomycetes possess no definite ascocarps, but the asci are scattered singly over the mycelium or the surface of the substratum (Fig. 179, *A*), so that not even a hymenium is formed. In the more advanced types of Ascomycetes, the ascocarp consists of the hymenium (asci and paraphyses), together with such sterile parts or structures as may be present, most of which are concerned with the protection or the dissemination of the spores. In the more familiar types, the hymenium at maturity is exposed as the inner lining of a cup-shaped or saucer-shaped ascocarp known as an **apothecium**. The base and side walls of the cup are of sterile tissue. Sometimes this cup is produced on a distinct

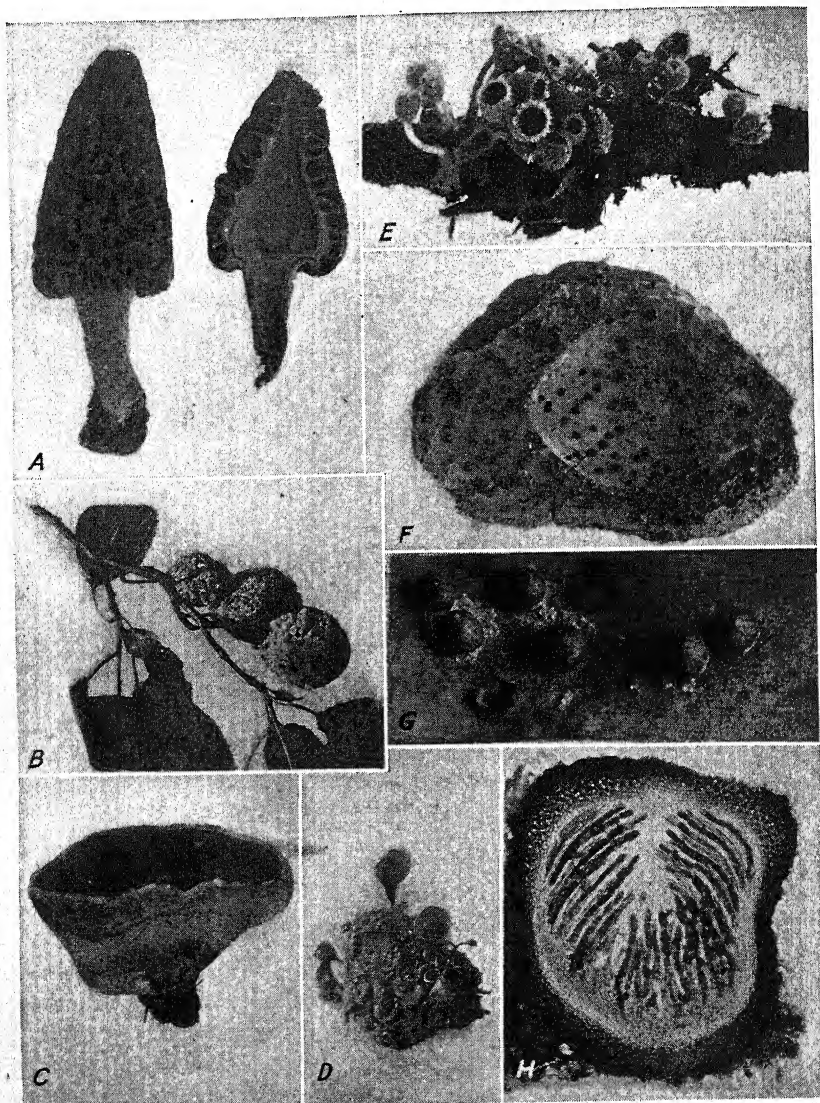


FIG. 181. A, a species of morel; B, plum fruits infected by the brown-rot fungus; C, a cup-shaped apothecium of the genus *Peziza*; D, apothecia developing from a brown-rot "mummy"; E, a common cup fungus (*Sarcoscypha occidentalis*) with scarlet hymenium and covered externally with long white hairs; F, perithecia growing saprophytically on the inner surface of a peach pit; G, perithecia of the peach-pit fungus enlarged to show the apical ostiole; H, section through a perithecium-like structure of another genus, showing heavy black wall of the perithecium and the internal, elongated asci. (D, photograph by Dr. C. S. Parker.)

stalk or stem, making the entire ascocarp appear goblet or urn shaped. Ascomycetes with this type of ascocarp are sometimes known as the "cup fungi" (Fig. 181, C-E). In others, the ascocarp is a rounded or flask-

shaped body with or without a small opening for the escape of the spores, which are produced, therefore, in internal asci. This type of fruiting body is known as a **perithecium** (Fig. 181, F-H).

The Imperfect Stage. In addition to the perfect stage in which ascospores are produced, there is frequently another reproductive phase known as the imperfect stage or conidial stage, in which one or more types of conidia or asexual spores are formed. These are always produced at the ends of special simple or branched hyphae known as conidiophores. They are quite analogous to the conidia formed in the Phycomycetes, although

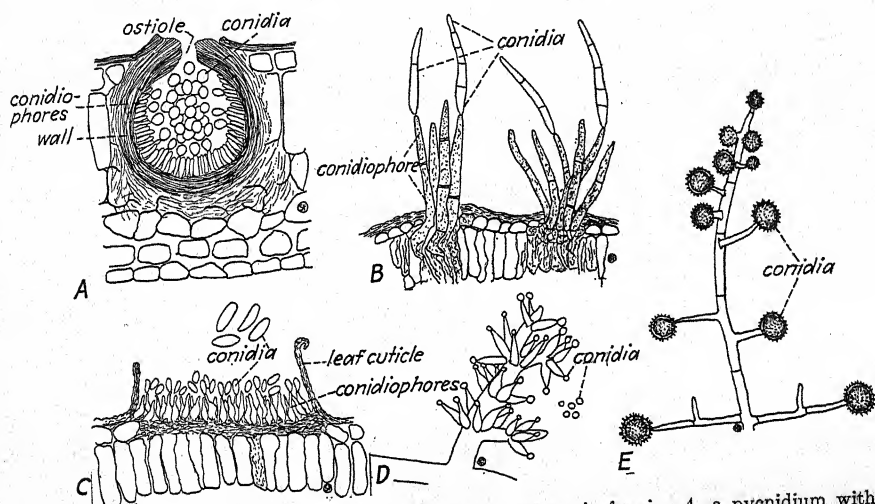


FIG. 182. Different types of conidial or imperfect stages in fungi. A, a pycnidium with dense hyphal wall lined with conidiophores and producing globose conidia that escape through the ostiole; this pycnidium is buried in the leaf tissue of its host; B, septate conidia produced on erect clustered conidiophores that protrude from the leaf tissue; C, an acervulus type of fruiting body with conidia, on conidiophores arranged in a definite layer below the leaf cuticle; D, E, conidia, produced at irregular intervals on branches of the mycelium. (Drawings by Edna S. Fox.)

they always germinate by a germ tube. Comparable with the three types of distribution already described for the asci, the conidiophores may be (1) scattered irregularly over the mycelium (no hymenium formed) (Fig. 182, D, E), (2) aggregated into exposed flat or saucer-shaped fructifications comparable with apothecia in form, and known as **acervuli** (Fig. 182, C), or (3) grouped into definite or rounded bodies with or without an opening to the exterior, comparable with the perithecium and known as **pycnidia** (Fig. 182, A).

The spores produced in this stage serve to disseminate the fungus rapidly throughout the growing season. They are usually short-lived, while the ascospores, or at least the ascospore stage, often represent a resting stage in the life history and serve to tide the fungus over the winter.

Spore Discharge and Dissemination. Ascospores are usually discharged from the asci by means of some internal force that projects them into the air where they are caught up by air currents and disseminated. A visible example of this discharge can be observed in any of the larger cup fungi, where, if the plants have been undisturbed for some time, a slight jar or the blowing of the breath on the hymenium is sufficient to cause a distinct cloud of spores to be thrown out of the asci and to disappear into the atmosphere.

In the imperfect stage, no such violent discharge is known to take place. The spores are disseminated singly as they ripen and fall off the conidiophores or they are forced out in coils through the opening in the pycnidial wall. In the latter case, rain plays an important part in dissolving and scattering these spore coils and washing them from one place to another. Under other circumstances, birds, beetles, and other insects are known to play an important part in incidentally aiding in spore dissemination.

Sexuality in the Ascomycetes. The problem of the sexuality of the Ascomycetes has received much attention in recent years, and, while many points still need investigation, the important outlines have become comparatively clear. A general conclusion that can be drawn from these researches is that sexuality is on the decline in the group. Consequently the range is from a well-defined heterogamy, comparable with that in the Phycomycetes or the algae, to complete suppression of the sexual organs, though perhaps there always remains a fusion of nuclei representing the essentials of a sexual process. Three stages in this sexual evolution may be cited:

1. *Both Antheridia and Oögonia Present and Functional.* *Pyronema confluens* is a small type of cup fungus, very common on sterilized and heated soils. In this species the oögonia (ascogonia) originate in clusters from the tips of erect hyphae (Fig. 183, A). The individual oögonium is at first club-shaped and multinucleate. Each oögonium is situated on one or two small basal cells. At the tip of the young oögonium there is produced a small beak which is soon cut off from the body of the oögonium and which elongates into a tube-like process known as the trichogyne. The basal part, *i.e.*, the oögonium proper, soon becomes balloon-shaped and contains at maturity as many as one hundred nuclei.

The antheridia arise from another hyphal branch, are clavate in shape, and multinucleate (Fig. 183, A), containing also close to one hundred nuclei. One or more of these antheridia grow upward and come into contact with the tip of the trichogyne. A passageway is dissolved between the two organs at the point of contact, and at about the same time the basal wall of the trichogyne breaks down so that there is a continuous passageway from the antheridium into the oögonium. The content of the antheridium

flows through this passage and mingles with the content of the oögonium. The sex nuclei then arrange themselves in pairs within the oögonium, but probably no fusion occurs at this time. Instead, there begin immediately to grow out from the wall of the oögonium numerous tube-like outgrowths, the **ascogenous hyphae**, or ascus-bearing filaments. Into these outgrowths the paired nuclei migrate, one pair into each hypha. This is regarded as the beginning of the sporophytic generation. These hyphae elongate rapidly, all taking an upward parallel direction of growth (Fig. 183, B). The pairs of nuclei divide repeatedly during this growth, and cross walls divide the hyphae into cells each containing a descendant of both of the original sex nuclei. Eventually, this growth stops, and the binucleate tip cell or the cell immediately behind it proceeds to form the ascus (Fig. 180,

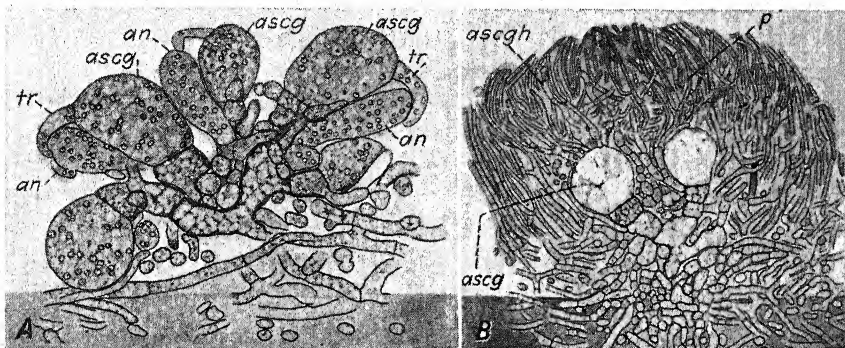


FIG. 183. Sexual reproduction in *Pyronema*. A, development of antheridia and oögonia; *an*, antheridium; *ascg*, oögonium or ascogonium; *tr*, trichogyne; B, development of ascogenous hyphae from the oögonia; *ascg*, oögonium; *ascgh*, ascogenous hyphae; *p*, paraphysis. (After Claussen.)

A-H). The nuclei in the young ascus fuse, as previously described, and the fusion nucleus, by a series of three successive divisions, gives rise to the nuclei for each of the eight spores that are then cut out. As stated previously, one of these divisions is a reduction division and marks the end of the sporophytic phase and the beginning of the gametophytic phase.

While this is taking place, the cells at the base of the oögonia and antheridia send out hyphae, some of which grow up to form a membrane-like outer wall around the ascogenous hyphae. Others grow up between the ascogenous hyphae to form the paraphyses already described. This completes the growth of the ascocarp, the hymenium being the combination of asci and paraphyses, and the surrounding sterile tissue having come from hyphae originating below the sex organs. The product of several or many antheridia and oögonia may be combined into a single ascocarp.

The fusion of the two nuclei in the young ascus constitutes fertilization.

Even though the nuclei that fuse are not the original sex nuclei, they are their descendants, the original nuclei having divided several times to furnish nuclei for all the other cells of the ascogenous hyphae.

2. *Oögonium Present; Antheridium Absent.* In *Lachnea scutellata* and other species the course of development is somewhat different. Early in development, there is differentiated a short hypha of seven to nine large cells, of which only the one next to the apical cell is an oögonium. It is multinucleate. No antheridium is formed. The oögonium gives off ascogenous hyphae, the cells of which are at first multinucleate but eventually the terminal cells become binucleate, and the asci arise from these. This development parallels that described above except for the absence of the antheridium. The nuclei that eventually fuse have had a common origin in the oögonium and one of them must be regarded as a

substitute for the male nucleus. The details of nuclear division in the young ascus are as described in the previous paragraph.

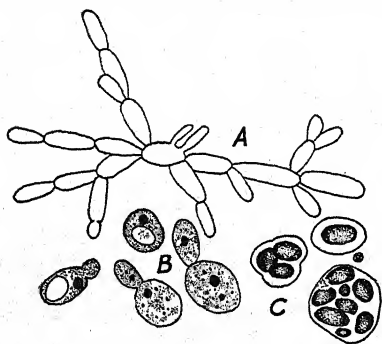


FIG. 184. A yeast plant. A, filament of cells produced by the budding process; B, single cells in the process of budding; C, cells that have become asci, containing from one to eight spores. (Drawing by Edna S. Fox.)

3. *No Recognizable Sex Organs Present.* In *Helvella elastica* there is no differentiation into sex organs. All the hyphal cells are multinucleate and from certain of these purely vegetative cells the ascogenous hyphae arise. Their cells are at first multinucleate but, by the time the asci are ready to be formed, the tip cell, at least, has become binucleate, and the asci and spores are formed as in the previous cases.

Classification and Features of Special Interest. No attempt is made here to present a complete classification of the Ascomycetes. Only those groups of more or less biological interest are included.

Yeasts and Related Ascomycetes (Order Saccharomycetales). While the yeasts are unicellular plants, they are universally recognized as Ascomycetes, supposedly of a simplified or degenerate type. They usually reproduce by a budding process (Fig. 184, A, B), but under other conditions the entire cell becomes an ascus, the protoplasm being divided between usually one to four spores (Fig. 184, C).

Yeasts are of considerable economic importance. They are able to cause extensive fermentation processes in carbohydrate solutions, with the attendant production of alcohol and the release of carbon dioxide. In this way, wines from grapes and berries, fermented cider from apples, and beers

from sprouted barley are obtained. It is not always necessary to add yeast to the solutions containing the fruit sugars since desirable wild yeasts are often present on the exterior of the fruits. The alcoholic content of the resultant liquids is low, usually less than 15 per cent. If present in greater concentration, the fermenting organisms will be rendered inactive. These fermentation processes are simply a part of the respiratory process of the organism, carried on by means of enzymes that they are able to produce. The same principle underlies the use of yeasts in breadmaking. Owing to the fermentation of the sugars in the dough, alcohol is formed that is driven off by the heat of baking, and the carbon dioxide that is released "raises" the bread in making its escape. While nearly all yeasts are capable of causing the fermentation of carbohydrates, only a few species are actually used by man. The others are often referred to as "wild yeasts." They are very widely distributed in nature.

Another group, often classed with or near the yeasts, includes species that are parasitic in the tissues of living plants. Perhaps the most important of these is the one causing a disease known as "leaf curl" on the leaves of peach trees. The leaves become much curled, thickened, and distorted and are of a yellowish color. The asci are produced singly on the surface of the diseased leaves (Fig. 179, A). The annual loss attributed to this disease in the United States runs into millions of dollars and is caused by the reduction of the amount of photosynthetic tissue available for food manufacture and a consequent reduction in the peach crop. This loss is largely preventable, since it is known that the fungus winters over mostly in the ascospore stage. These spores lodge in the crevices of the bark on the trees or in bud scales and are easily destroyed by a so-called "dormant spray" applied 2 weeks before the buds begin to unfold. Bordeaux mixture and lime-sulfur sprays are efficient in this respect, the chief point being the necessity for thorough work in their application.

Blue and Green Molds (Order Aspergillales). This is rather a heterogeneous order best known through those genera, such as *Penicillium* and *Aspergillus*, the species of which develop as green or black (rarely yellow or reddish) molds on various organic substrata, such as oranges, lemons, preserved fruits, and ensilage. Several species cause characteristic changes and flavors in dairy products and are used in the ripening of cheese. In fact, the distinct flavors of the various types of cheese are due to the presence of distinct species of these molds. Other species of the same genera are known to cause diseases in animals, especially in birds and man. A peculiar skin affliction, known as the Tokelau disease, common to the natives of the South Sea Islands and resembling the ringworm disease in appearance, is caused by a fungus belonging to this group. As previously stated, the antibiotic penicillin is obtained from *Penicillium notatum*.

In the common blue and green molds of citrus fruits, the fruiting stage usually observed is a conidial stage with spores produced in chains on special conidiophores (Fig. 185, *B*). Asci in delicate, thin-walled perithecia are rarely developed (Fig. 185, *A*) and in most species are unknown.

Cup Fungi (Order *Pezizales*). This is one of the largest orders of the fungi, containing about five thousand species commonly referred to as the cup fungi, since the ascocarp is an apothecium or cup-like body, often mounted on a distinct stalk (Fig. 181, *C-E*). Undoubtedly, many of the larger forms are edible but this point has not been well investigated. *Peziza* is a common genus, with many species occurring as saprophytes on decaying vegetable matter or on the ground. All have rather large fruiting bodies, often as much as 4 in. in diameter, and more frequently saucer-shaped than cup-shaped. Some are brilliantly colored. The hymenial

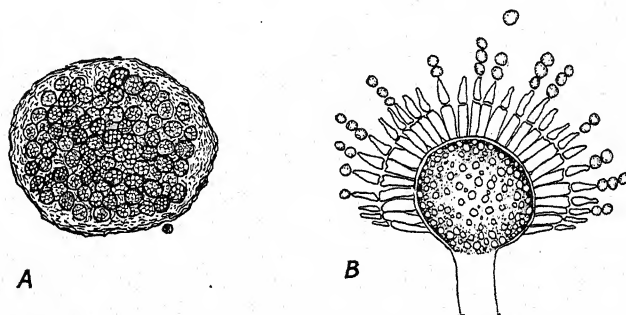


FIG. 185. *Aspergillus*. *A*, a thin-walled delicate perithecium containing numerous asci with spores; *B*, section through a single globose conidial head, showing the pointed radiating spore stalks and the conidia produced in chains. (Drawing by Edna S. Fox.)

layer of asci and paraphyses lines the cup on the inside. The asci are cylindric or club-shaped and nearly always contain eight spores.

A few species are of economic importance. Perhaps the one (*Sclerotinia cinerea*) causing the "brown rot" of such stone fruits as cherries, plums, and peaches is the most important one. In wet seasons, in particular, these fruits become brown and soft, and a mold-like growth develops over them (Fig. 181, *B*), sometimes destroying 50 per cent of the crop over wide regions. The rot also develops on the fruits in storage and in transit, the mycelium under the influence of the moisture in the container spreading rapidly from fruit to fruit. On the tree, the fungus is spread rapidly by conidia that are produced on the mold-like growth on the rotting fruits. The fruits of the peach and plum, so attacked, often dry up on the trees, and in these "mummies" the fungus hibernates over winter. In the spring, the mycelium grows out from these fallen mummies to produce an ascocarp of the cup-fungus type (Fig. 181, *D*) in which are produced the

ascospores that may infect the next crop. The fungus also attacks the flowers and gains entrance to the twigs, where it is perennial and may form conspicuous cankers. In the control of this disease, it is advisable to get rid of all mummies, especially since the mycelium in this stage may remain dormant for several years. The correct application of a lime-sulfur spray will also control it.

A great many species of the cup fungi are parasitic on the simpler members of the green and the blue-green algae and are sometimes referred to as lichens.

Morels and Truffles (Orders Helvellales and Tuberales). One genus, *Morchella*, of the Helvellales is rather well known as an edible mushroom under such names as "morel," "sponge mushroom," "spring mushroom," "haystack mushroom," "hickory chickens," and other descriptive titles. These are the largest ascocarps of the entire Ascomycete groups, sometimes growing a foot tall and weighing up to about 1 lb. There are several species in the genus, most of which do not reach these larger measurements but are only 2 to 4 in. tall. To the mushroom lover, no species surpasses these in their culinary delicacy. The ascocarp consists of a hollow stem bearing a somewhat conical enlarged upper portion that is marked with ridges and furrows (Fig. 181, A). In the furrows the hymenium develops. These mushrooms may be found about the time the apple trees are in bloom. Indeed, an old apple orchard is one of the best places to find them, though they occur just as abundantly in sandy soil along creeks and rivers or along old fence rows where the soil is rich and sometimes in open oak and hickory woods. In Europe the species of this genus are sold, in season, on all the principal city markets. In this country they are less well known, but in the Missouri and Mississippi River valleys they are gathered in large quantities along the river bottoms and disposed of on the local markets.

The members of the order Tuberales are entirely subterranean fungi and the ascocarps are commonly known as truffles. They are rounded in form, usually brown or black in color, and rather rough on the outside. The asci and spores are borne internally, the hymenium lining internal passageways that usually open to the exterior by one or more pores or mouths. There are less than one hundred species of this order and about half of them are in the single genus *Tuber*. They are edible fungi and in France, Spain, and Italy they form an important article of commerce. In size, they vary from the size of a pea to 4 in. in diameter and weigh as much as a pound. They grow apparently in close association with the roots of certain trees, particularly oaks and chestnuts, on which they are probably somewhat parasitic. The ascocarps are buried just beneath the surface of the soil or under leaves and are easily dug out when once located. A keen observer,

after some practice, can find them unaided by taking careful note of the situations in which they grow. Usually, however, they are gathered with the assistance of trained dogs or trained pigs. In the latter case the female is said to be a better truffle hunter than the male. These animals locate them by their odor, which is said to be quite characteristic. Pigs are quite fond of them and root them out with great efficacy. As an article of commerce, truffles are to be found, in season, on all the important markets of southern Europe. In France, they are canned for export.

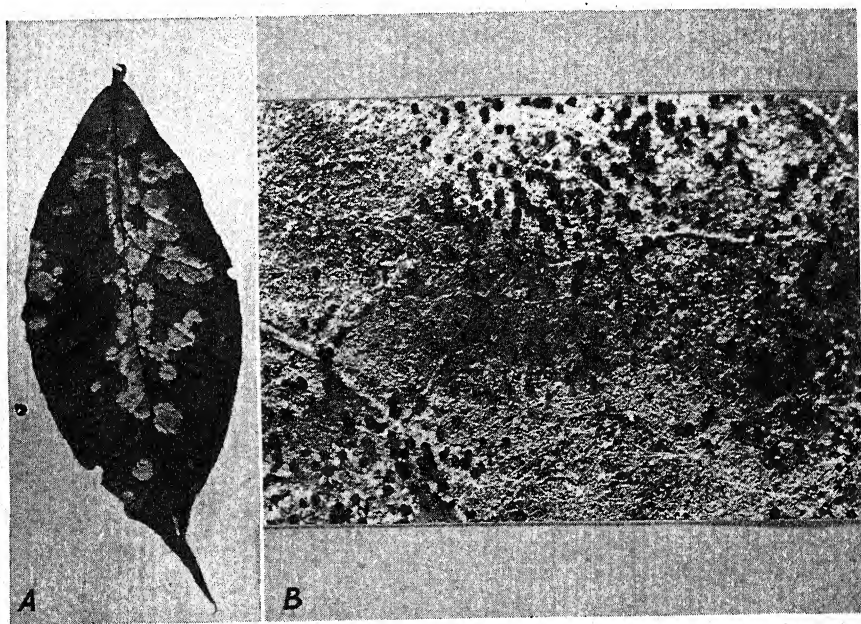


FIG. 186. Powdery mildew of *Phlox*. A, leaf of *Phlox* showing white mildew patches on its upper surface; B, photograph of small area of infected leaf surface, magnified to show the globose black perithecia.

In America, truffles occur mainly on the Pacific Coast, though a few have been found in the East, particularly in New Jersey and Pennsylvania, in Michigan, and in Minnesota. They have never been found in quantity. All American species, numbering about 25, are said to be of yellowish or white color.

Powdery Mildews (Order Perisporiales). This order is unique among the Ascomycetes in developing a mycelium that is largely superficial on the substratum or the host. Most of the species, however, are parasitic, at least sending absorbing organs (haustoria) into the epidermal cells of the host. The order includes two groups known in popular terms as the powdery mildews and the sooty molds. The former group has a white or

gray mycelium and the latter a dark-brown or black one. In both cases, the fruiting body is a perithecium often completely closed and frequently with hyphal appendages of peculiar and characteristic form.

During the growing season, the powdery mildews form a gray or white coating on the surfaces of the leaves they attack (Fig. 186, A). The appearance may at times be powdery, owing to the formation in large

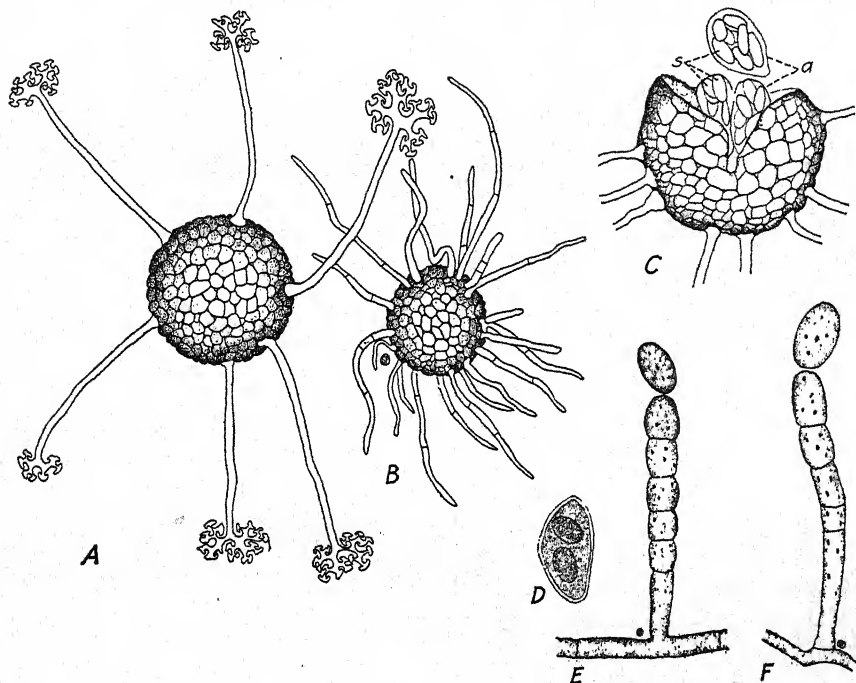


FIG. 187. Reproduction in powdery mildews. A, B, perithecia of two different species of mildews; note cellular walls of the perithecia and the elongated appendages with dichotomously divided tips in A; C, perithecium partially burst open, showing the contained asci, *a*, with their ascospores, *s*; D, a single ascus with two spores; E, F, mycelial branches dividing into chains of conidia. (Drawing by Edna S. Fox.)

numbers of the conidia that are cut off in chains from the tips of erect hyphae (Fig. 187, E, F). Since these spores serve to distribute the fungus very rapidly to other hosts of the same species, the mildews are likely to spread very rapidly during the summer. Late in summer or in autumn, the perithecia are formed on the same mycelium and appear as minute black dots scarcely visible to the unaided eye (Fig. 187, B). In these the spores are formed in asci (Fig. 187, C-D), but they are not liberated until the following spring when the perithecial wall disintegrates. The spores are disseminated in time to infect the foliage for that season. The cellular

walls of the perithecia are provided with peculiar elongated appendages (Fig. 187, A, B).

Dusting infected plants with flowers of sulfur has proved to be the most successful method of combating these diseases, some of which, such as the mildew of the rose (*Sphaerotheca pannosa*), of the apple (*Podosphaera oxycanthae*), and of the wheat (*Erysiphe graminis*), are sometimes of considerable economic importance.

Higher Ascomycetes (Orders Hypocreales and Sphaeriales). The characteristic feature of the first-named order is the bright color and the waxy consistency of the perithecial fruiting bodies. The colors vary from white to yellow and red. Many are parasitic, sometimes on other fungi or on

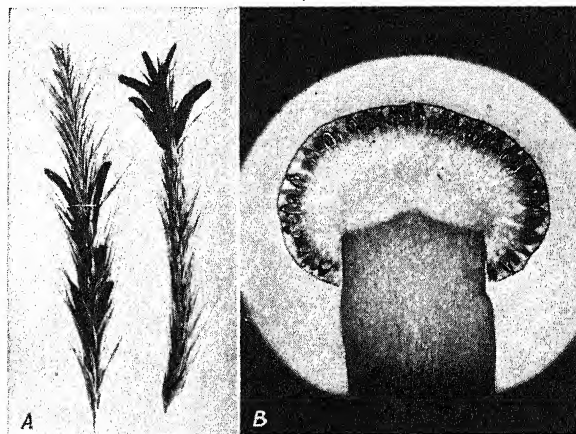


FIG. 188. *Claviceps purpurea*. A, sclerotia replacing grains in head of rye; B, photomicrograph of vertical section through the stalked knobs which arise from sclerotia; the circle of elongated cavities toward the periphery of the head consists of perithecia that contain asci.

insects or the pupae of beetles; very few take first rank as highly destructive parasites of economic importance.

The genus *Claviceps* is of some economic importance. Its species are parasitic on various grasses, including rye and barley and occasionally wheat. The fungus is first observed as a hard, black, cylindric sclerotium known as an **ergot** that entirely replaces a grain in the fruiting head (Fig. 188, A). These sclerotia are resting stages and the next spring give rise to small stalked knobs in which are embedded numerous perithecia which produce the spores in asci (Fig. 188, B). The ascospores produced in this stage are disseminated and are capable of infecting the ovaries of the grasses. Here the mycelium grows for a time, meanwhile cutting off a type of conidium capable of spreading the fungus to other hosts. Eventually the mycelium entirely destroys the ovary and organizes in its place the sclerotium.

Grasses heavily infected with *Claviceps* should not be used for pasture or for hay, since the fungus in the sclerotium stage is poisonous to stock, inducing a diseased condition in which the animals become emaciated and often covered with sores, while in extreme cases parts of the tails or ears may be entirely sloughed off, and abortion may occur in females. In case the ergots are mixed with the seed intended to be used for sowing, they can be easily removed by immersing the seed in vats of 20 per cent salt solution, in which the seed will sink to the bottom and the ergots will float on top and can easily be skimmed off. Extracts of ergot are widely used in medicine.

The fungi in the second order are separated from those of the first by the usually black, carbonous character of the perithecia. This is the largest of the orders of Ascomycetes and its species are probably the most common of all the members of the class. They are to be found on every dead stick in the woods, as well as on a variety of other plant materials, usually appearing as black spots or crusts, more rarely as finger-like projections from the substratum (Fig. 189, *E*). Most of the fungi in this order produce two types of spores, conidia and ascospores, with their usual distinct functions.

The genus *Endothia* includes the fungus *E. parasitica*, causing the blight of the chestnut tree (Fig. 189, *C*). This disease was apparently introduced from China about 1900 and has virtually destroyed all the chestnuts in the United States. No measures of control suitable to the situation are known. The fungus has two spore stages, ascospores, produced in perithecia, and conidia, produced in fruiting bodies known as pycnidia. The fungus mycelium is parasitic on the cambium and the living cortex cells of the tree.

A host of other species causes plant diseases of various sorts, some of great economic importance. The black rot of grapes, black knot of cherry and plum (Fig. 189, *F*), a leaf spot of strawberries (Fig. 189, *D*), twig blight of sycamore (Fig. 189, *G*), a black rot and canker of apple, and apple scab (Fig. 189, *B*) are only a few of the most important ones. These diseases are all subject to control by modern methods of spraying, the details of materials and application varying with the life history of the individual parasite.

Lichens (Order *Ascolichenes*). Many Ascomycetes are found growing in close association with one of several genera of green or blue-green algae. Associations of this sort represent a type of symbiosis to which the name *lichen* has been applied. Some writers regard this as a case of so-called mutualistic symbiosis in which both of the participants are benefited. Others, probably with considerably more reason, regard the relationship as one of parasitism, the fungus being parasitic on the alga with which it is associated, as evidenced, at least in some cases, by the presence of fungous haustoria in the algal cells. *Protococcus* or a closely related genus (*Cystococcus*) is the alga usually involved, though in some cases blue-green algae (*Nostoc*,

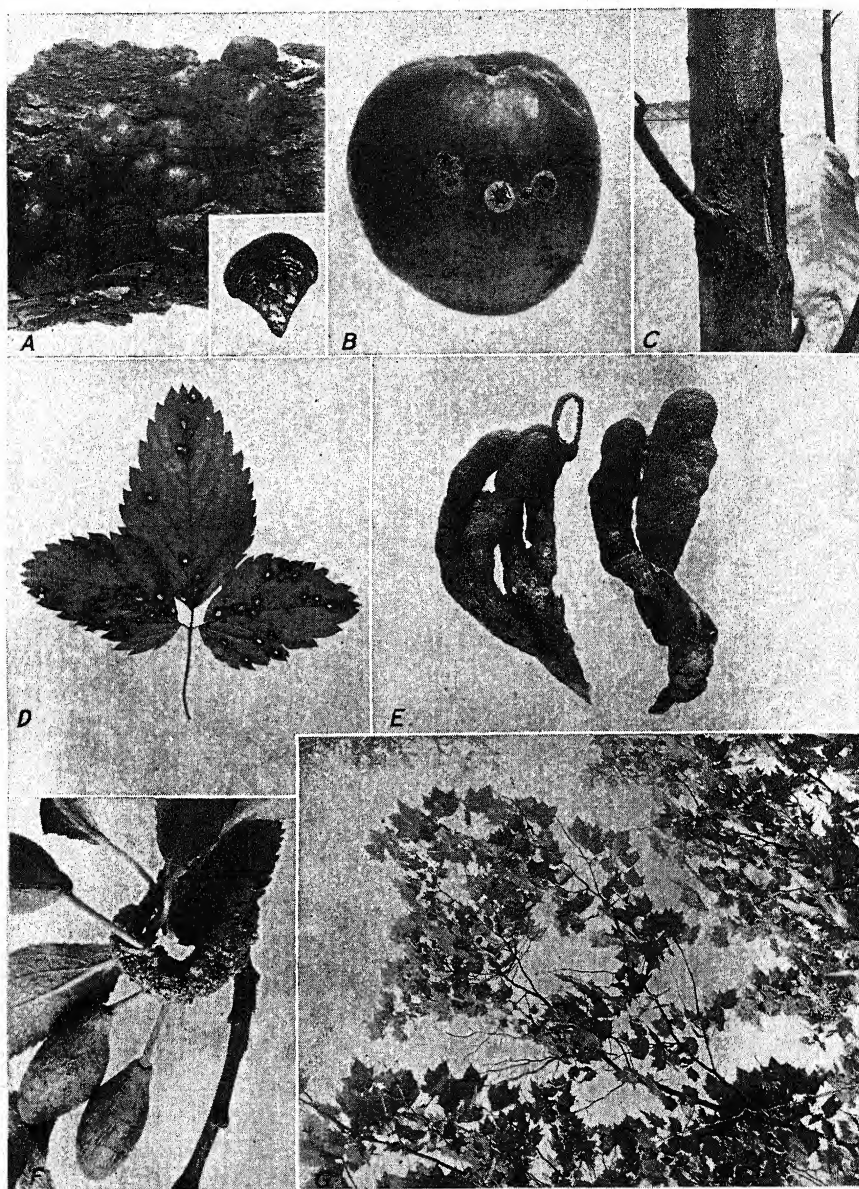


FIG. 189. Various types of higher Ascomycetes or the diseases they cause. *A*, a common black charcoal-like fungus (*Daldinia concentrica*) found on old logs; perithecia are imbedded near the periphery of these masses; *B*, apple scab, caused by *Venturia inaequalis*; *C*, chestnut blight, caused by *Endothia parasitica*; *D*, leaf spot of strawberry, caused by *Mycosphaerella Fragariae*; *E*, "dead man's fingers," the fruiting structures of *Xylaria polymorpha*; *F*, the black-knot disease of plum, caused by *Plowrightia morbosa*; *G*, photograph of a portion of the crown of a sycamore tree, showing numerous small dead branches killed by *Gnomonia veneta*.

Gloeocapsa, and *Rivularia*) are found in similar relationships. Such algae are able to reproduce themselves, at least to some extent, in this symbiotic relationship, by cell division. The fungus may likewise reproduce itself, at least to some extent, by ascospores formed in asci, contained in cup-like apothecia or in perithecia (Fig. 191, A, B). Probably these spores are not usually able to reproduce the fungus unless, when they germinate, they come into contact with free-living algal cells. This may be, therefore, a case of obligate parasitism so well illustrated in the powdery mildews, the downy mildews, the rust fungi still to be considered, and many others. Special reproductive bodies known as *soredia* are also present. These consist of definite masses of fungous hyphae containing embedded algal cells that are cut out and break off to continue growth in a new location.

In general, the fungus hyphae of the association so completely surround the alga that in an examination of a section through such an association the algal cells are found deeply embedded in fungus mycelium (Fig. 190). This of itself must place the alga at some disadvantage in obtaining the sunlight necessary for photosynthesis.

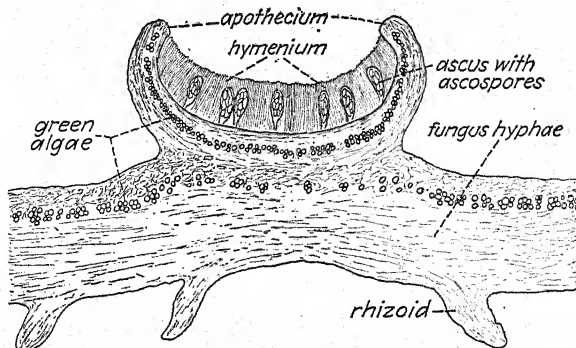


FIG. 190. Diagrammatic representation of a cross section through an apothecium fruit on a foliose lichen thallus. (Drawn by Ernest Geisweide.)

These associations of algae and fungi are conspicuous and widespread. They are found in abundance everywhere on tree trunks, especially on the shaded sides; they occur on exposed rocks (Fig. 191, A, B) where no other vegetation, except perhaps the alga of the association, could grow; they occur on old logs and on the ground in woods. In fact, they are likely to develop in any position capable of sustaining plant life. In damp woods of warm regions, they often hang in long festoons from trees; in the arctic zones they develop as cushion-shaped masses on the ground, where they often form an important food of the reindeer.

In form, three different types of lichens are recognized. The most common and most conspicuous is the foliose type, in which the body has the form of an expanded thallus, often not unlike a thallose liverwort (Fig. 191, A). Such thalli usually bear, at some time, on their surfaces the apothecia of the fungus, in which asci and spores are produced, as in *Peltigera*, *Physcia*, *Parmelia*, and other genera. Another type is the fruticose type (Fig. 191, C, D), in which the body is erect and often intricately and beautifully branched. Ascocarps of the apothecial type, but usually not definitely cup-shaped, often occur as bright-red expansions at the tips of some of the branches, as in species of *Cladonia*. The third type is the crustose type (Fig. 191, B), in which the body is a very thin crust entirely adnate to the substratum. Such types may bear

apothecia but more frequently the fungus fruiting body is a perithecium which is visible as a small globose body on the surface.

Lichens are of some economic importance. Their growth on bare rock initiates the weathering away of such rocks into soil particles, although the process is extremely slow. In arctic regions, certain species are very abundant, and because of the lack of competition of other plants they become an important portion of the flora, replacing as food, for such animals as the reindeer, the grasses of more southern regions. To a slight extent lichens are said to be used as food by man in arctic or northern regions

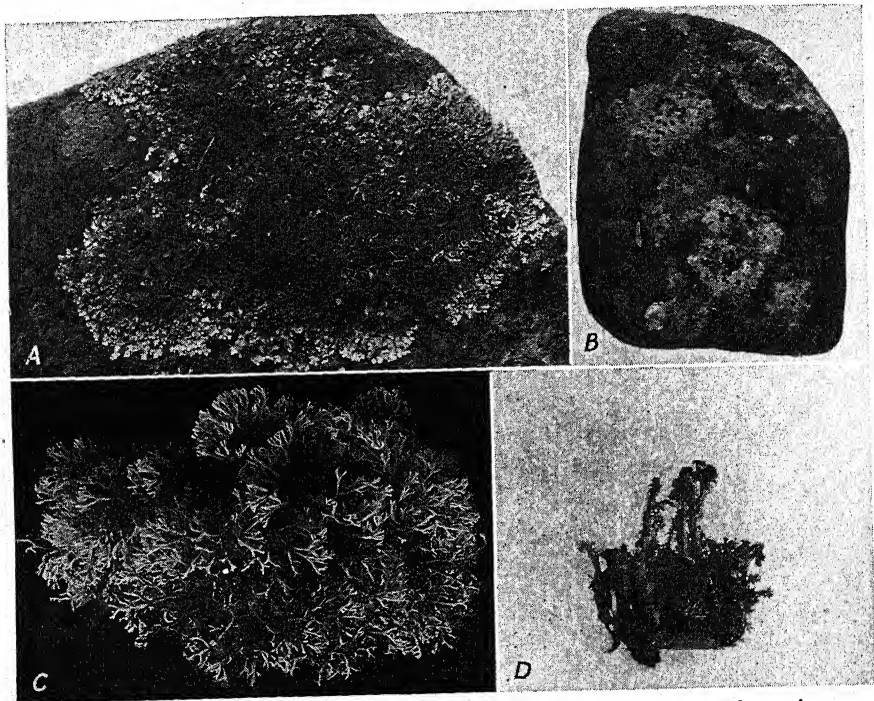


FIG. 191. Types of lichen thalli. A, a foliose thallus, bearing apothecia, and growing on a rock; B, a crustose thallus (white area) inseparable from the rock substratum and bearing small black perithecia; C, D, two species of the genus *Cladonia*, representing the fruticose type of lichen thallus.

where food is scarce. Dyes of different colors have been obtained from lichens but seldom in commercial quantities. Litmus solution is made by grinding up the plant body of *Rocella tinctoria* and extracting the coloring matter, after which paper is soaked in the neutralized solution and is then known as litmus paper.

It should be mentioned that the fungi of some lichens are Basidiomycetes, or imperfect fungi, and the other organisms of the association sometimes are autotrophic bacteria.

Summary of Ascomycetes. The Ascomycetes comprise a homogeneous group of fungi with the ascus as the characteristic feature of the group.

Other organs of various types may produce asexual spores termed conidia. Asci arise, often in conjunction with a sexual process, as terminal or sub-terminal cells of special ascogenous hyphae. In the ascus there is a fusion of two nuclei that are not sperm and egg but the descendants of sex nuclei or at least are to be regarded as possessing the potentialities of sex nuclei. Following fusion in the young ascus, three divisions usually occur, resulting in the formation of eight nuclei, each of which usually becomes the nucleus of an ascospore. One of the three divisions in the ascus is a reduction division. The sporophytic phase of the life cycle is regarded as originating with the association of two nuclei in the ascogenous hyphae and ending with the reduction division following nuclear fusion in the young ascus. Many species of Ascomycetes cause destructive plant diseases; a few cause diseases of animals; some are of economic importance in several commercial processes; a few are edible; many others are of no special importance to man. Finally, various Ascomycetes are found in close relationship with algae, forming those associations which are usually designated as lichens.

BASIDIOMYCETES

This is the class of the more conspicuous fungi, including the smuts, the rusts, mushrooms, toadstools, bracket fungi, puffballs, and many other kinds. It is quite a heterogeneous group; yet its members possess one feature in common: all species develop structures known as **basidia**, each of which usually produces four external spores. Most frequently the basidium is club-shaped and, like the ascus of the preceding group, it is the modified terminal cell of a hypha. The basidia vary considerably in structure (Fig. 201, A-D), some being transversely four-celled, some longitudinally four-celled, and many more one-celled. Usually the spores are produced on little stalks, known as **sterigmata**, that elevate the spores slightly above the level of the basidium. Spores produced on basidia are known as **basidiospores**.

Two rather well-marked groups of the Basidiomycetes may be recognized. The **lower Basidiomycetes**, including the rust and smut fungi, are strict parasites for at least a portion of the life cycle, while the **higher Basidiomycetes**, including the fleshy and woody forms usually known as mushrooms and toadstools, are usually saprophytic. Members of the former group have a basidium transversely divided into four cells, while in the latter group the basidia are either longitudinally four-celled or one-celled (Fig. 201).

LOWER BASIDIOMYCETES

Order I. Ustilaginales (Smuts). *General Life History and Characteristics.* The smuts, constituting a group of about 400 species, are probably as well known as is any other group of fungi. The diseases they cause are

usually referred to as "smut" diseases. They receive this name from the black, soot-like masses of spores that are produced externally on the living host. The mycelium is septate, and during its parasitic existence it is found in most cases scattered throughout the host, though disappearing in older parts of the plant as it advances into the newer growth. In a few cases, as in the smut of corn, the mycelium is found only near the region of initial infection. In most cases, as in the common smuts of grain plants, it is intercellular, but haustoria are said to be developed in certain other

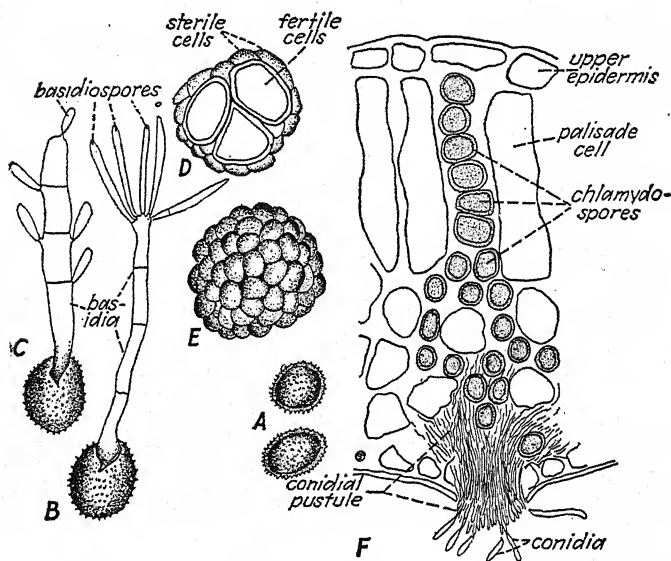


FIG. 192. Spores and spore germination in smut fungi. A, chlamydospores of corn smut; B, C, germination of smut chlamydospores and the formation of basidia and basidiospores; D, section through a smut ball of *Urocystis Agropyri*, showing the three fertile central cells and the surrounding layer of sterile cells; E, surface view of smut ball of *Sorosporium Everhartii*; F, section through a leaf of *Physalis* infected by one of the internal smuts, *Entyloma australe*.

species. In either case, though the host is seldom killed outright, its vitality is lowered and often a stunted appearance is evident. Eventually, the mycelium begins to mass at definite points and sometimes, as in corn smut, breaks out in the form of knobs or "tumors" (Fig. 193). These are at first white because of the colorless mycelium. Very quickly the mycelium at this point becomes transformed into a mass of dark-colored spores. In the simplest cases, the content of each hyphal cell rounds up internally and lays down around it a new cell wall. The spores so formed soon separate as individual units (Figs. 192, A, F; 194, D, E) or, in some species, remain in closely compacted aggregations of as many as one hundred cells

each, termed **spore balls** (Fig. 192, *D, E*). The spores are termed **chlamydospores**. Owing to their heavy walls they retain their vitality for several years, although in most cases they are capable of immediate germination. The chlamydospores themselves are usually not able to infect any plant, the infection taking place in the stage which follows.

When the chlamydospores germinate, usually the next spring, they produce a cylindric germ tube, the basidium, composed of one to four cells, and on one or more of these cells the basidiospores are formed (Fig. 192, *B, C*). The basidiospores are capable of infecting growing plants of the proper species by producing a germ tube that enters the tissues, usually through the stomata of the host.

In some species, conidia are also produced on the parasitized host (Fig. 192, *F*). Thus as many as three different spore types may occur in the life history. In a few species, neither conidia nor basidiospores are present, infection taking place by the germ tube produced when the chlamydospore germinates, as in one of the common smuts of wheat.

No sexuality involving functional sex organs is known to exist in these fungi. In some species, the basidiospores are known to conjugate in pairs before germination, but the significance of this process is in question. The nuclei of the conjugated spores do not usually fuse at this time, but the cells of the mycelium that is formed from such fused spores remain binucleate until, in the early stages of chlamydospore formation, fusion takes place. In other cases the host may be infected by mycelia from each of two uninucleate basidiospores. Cells of these mycelia, if in close proximity, unite and establish the binucleate condition which persists until chlamydospore formation.

There is, therefore, in the life history of most smuts, a binucleate phase that originates by cytoplasmic conjugations between certain cells. By a simultaneous division of the two unfused nuclei, each new cell that develops from these conjugated cells receives two nuclei. By this means the binucleate condition is maintained in the resulting mycelium. This is comparable with the binucleate condition of the ascogenous hyphae that was described as a part of the life history of many Ascomycetes (page 451). Eventually the descendants of these nuclei fuse when the mycelium develops into chlamydospores. This fusion suggests a similar one, described at the termination of the binucleate condition in Ascomycetes, in the young ascus. If this analogy is a true one, then the two nuclei that initiate the binucleate condition may be regarded as the equivalents of sex nuclei, one with male the other with female characters. Likewise, the two nuclei that fuse in the young chlamydospore would be sex nuclei, since each of them is a descendant of one of the two nuclei of the original fusion cell. Following the interpretation given in the Ascomycetes, the binucleate

mycelium and the chlamydospore, with its fusion nucleus, would represent the sporophytic portion of the life cycle. If, as might be expected, a reduction immediately follows this fusion, the resulting germ tube (basidium) and the basidiospores it produces would be the representative of the gametophytic generation, at least in those species where the binucleate condition originates from the conjugation of two basidiospores.

Special Types of Smuts—Economic Importance. Three types of smuts are recognized on the basis of the time of germination of the chlamydospores, coupled, of course, with the time of infection. These types are represented by the corn smut, the "loose

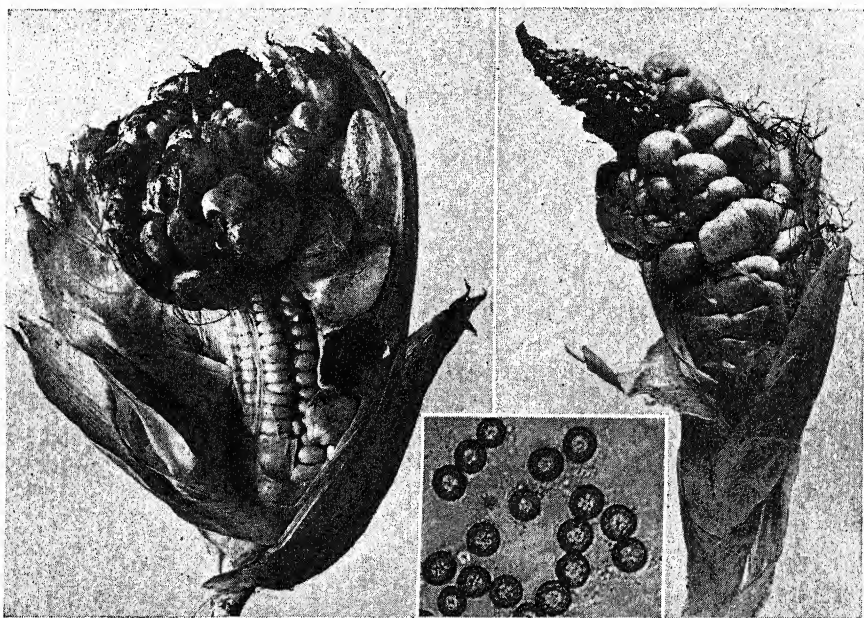


FIG. 193. Two ears of corn deformed by corn smut, the tumors unbroken on the right but broken and disseminating spores on the left; insert shows chlamydospores of corn smut.

smut" of oats, and the loose smut of wheat, each with a different type of life history and necessitating the use of different control methods.

In the smut of corn (*Ustilago Zeae*), the smut tumors that may appear anywhere on the aboveground portions of the plant are, at maturity, masses of black dusty chlamydospores (Fig. 193). These spores are matured during the summer or fall and usually lie dormant on the stalks, in the soil, or in other favorable places, although they are capable of immediate germination. In the spring or the following summer, they germinate in abundance, the period of germination for different spores covering several weeks of time. The basidiospores formed on the resulting basidia are capable of producing germ tubes that may infect any growing part of the corn plant. After the mycelium so formed grows for a while within the tissues of the host, it begins to mass together at definite points and breaks out as the well-known smut tumors.

These are at first glistening white but soon become black as the chlamydospores are matured. The loss in the United States due to corn smut, in preventing the development of ears and reducing the vigor of the plant, is estimated to amount frequently to as much as 100 million bushels of corn annually. No adequate and practical method of control is known. Since the spores winter over in the soil and on the fodder, returning corn to the same soil for two or more years in succession places the crop in close proximity to the source of the infection. Rotation of crops is, therefore, of importance in preventing the damage due to corn smut. The use of manure from stock fed on the fodder also tends to increase the disease.

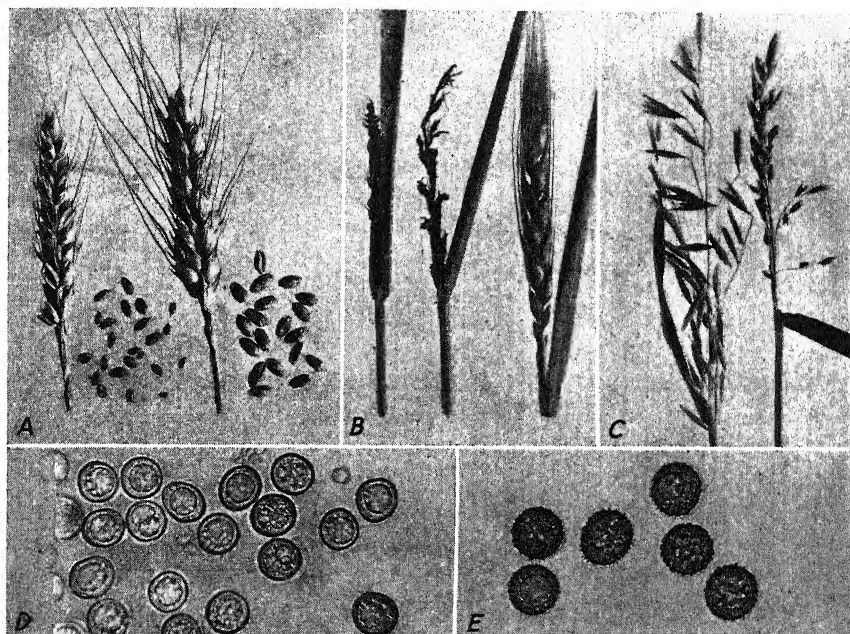


FIG. 194. A, stinking smut of wheat; infected head and the resulting grains on left, healthy head and grains on right. B, loose smut of wheat; two diseased heads on left, the entire head with exception of the rachis being destroyed; healthy head on right. C, loose smut of oats; healthy head on left, diseased head on right. D, E, photomicrographs of chlamydospores of the stinking smuts of wheat (*Tilletia foetens* and *T. Tritici*, respectively).

In the oat smut (*Ustilago Avenae*) and the "stinking smuts" of wheat (*Tilletia foetens* and *T. Tritici*) the spores produced on the smutted heads (Fig. 194, A, C) lodge on the healthy grains. They are able to germinate at once, but they retain their viability for periods of at least a year. When the grain is planted and germinates, the spores also start growth. Each spore produces a short germ tube which becomes the basidium (Fig. 195) and produces basidiospores. These immediately infect the very young seedling. The mycelium grows up with the plant, invading the new tissues as they are formed. Sometimes its effects on the young plants are so serious that they are very much dwarfed and never come to flower. As the host comes to the blooming and fruiting period, the parasite seems to become more aggressive and may entirely prevent the maturing of the flowers or may destroy only a limited number of the

ovaries. The loss in oats is estimated to run as high as 30 per cent of the crop in some instances, though perhaps more commonly not more than one-third of this. Practically all loss from both of these diseases is preventable except in extreme cases of heavy soil infestation, since it is possible to treat the seed with chemicals that will kill the spores lodged on the grain without affecting the viability of the grain. For this purpose formalin (formaldehyde) is highly effective for oats smut, the grain being sprayed or sprinkled with a solution made up of equal parts of commercial formaldehyde and water, and applied at the rate of 1 qt. of solution to 50 bu. of seed. The stinking smuts of wheat are controlled by dusting the grain with finely ground copper carbonate dust, prior to sowing.

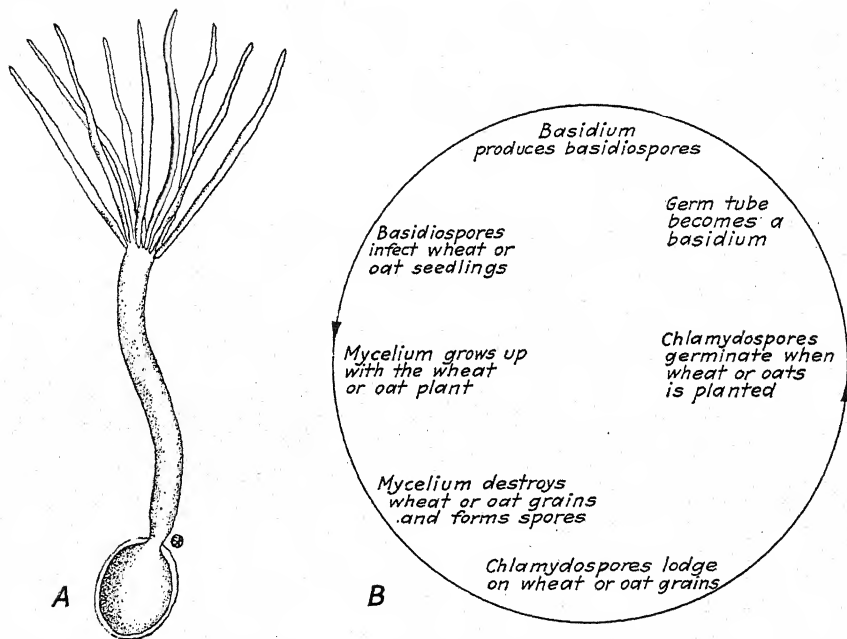


FIG. 195. A, a germinating chlamydospore of the stinking smut of wheat, with basidiospores at the apex of the basidium; B, a life-cycle diagram of the stinking smut of wheat and the loose smut of oats.

The loose smut of wheat (*Ustilago Tritici*) has a still different life history. About the time the healthy wheat plants head out, and shortly before they come into flower, a survey of almost any wheat field in which preventative measures have not been taken will show some smutted plants. These are usually not much or only slightly reduced in size as compared with healthy plants, but the head is found to be pushing out of the ensheathing leaves as a black powdery mass of chlamydospores (Fig. 194, B). These spores are carried to the healthy heads in flower. Here they germinate, the germ tube infecting the ovaries without producing basidiospores. There is no external evidence of this infection, except sometimes in the shriveled condition of the grain. Within the seed the mycelium lies dormant until planting time. When the embryo of the seed starts growth, the mycelium again becomes active, growing up through the plant as new tissues are formed, and by the time of flowering the head has been de-

stroyed. From the fact that the mycelium, if present at all, is within the seed at planting time, it is evident that seed treatment of the type recommended for oat smut cannot be effective. An efficient method of control has been developed, however, in the use of hot-water immersions for the wheat seed, the water to be maintained at a temperature of 125 to 129°F. for a period of 10 min. This treatment owes its efficiency to the fact that the mycelium of the fungus is killed at a temperature somewhat lower than that which would injure the embryo of the grain. It must be used with great care, however, since a temperature above 131° will injure the embryo, and temperatures lower than 123.5° are not effective against the fungus.

Order II. Uredinales (Rusts). *General Characteristics.* The term "rusts" has long been used to designate a great variety of parasitic or-

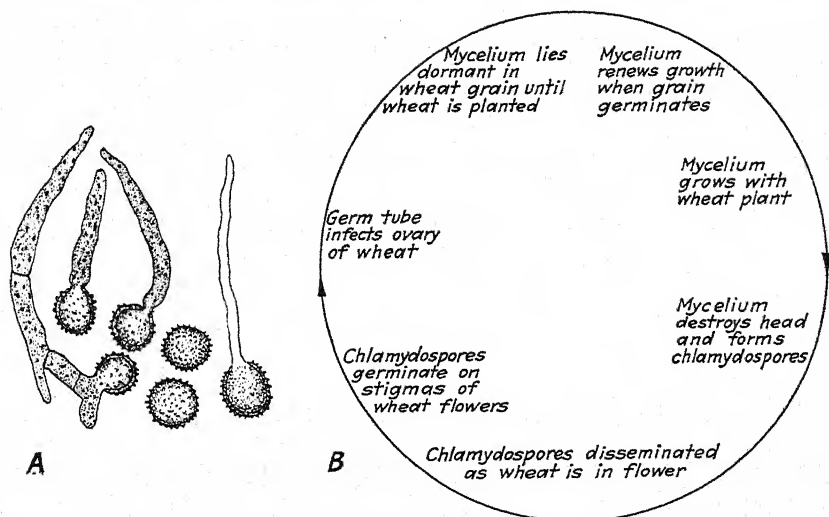


FIG. 196. *A*, germinating spores of loose smut of wheat; *B*, life-cycle diagram of loose smut of wheat.

ganisms that cause brown or rusty spots on living plants, particularly on the foliage. While there are many true rusts, at least a thousand American species, belonging to this order of the fungi, there are also many so-called rusts that belong to other groups. The true rusts agree with the smuts in some particulars, especially in being strict parasites and in producing a basidium directly from a spore, but they differ in the larger number of spore forms they may produce and in their brighter colors (yellow, orange, red, or brown).

All species of the order are highly specialized obligate parasites of seed plants and ferns, mostly unable to grow except on particular species of host plants or on a small group of closely related hosts. This high degree of specialization is emphasized by the fact that no one has yet succeeded in growing them in pure isolation cultures on an artificial medium.

As in the smuts, following infection of a host plant by the germ tube of a basidiospore, there is produced an internal mycelium ramifying either in local areas of host tissue or, as in the case of the so-called **systemic rusts**, pervading the entire plant aboveground, often producing marked dwarfing or distortion of the host plant. The mycelium is septate and is both intercellular and intracellular in position. When a hypha enters a host cell, it enlarges and often branches into special absorbing organs known as haustoria. When this vegetative phase of the parasite is well established, the mycelium begins to mass at points beneath the epidermis or, in some cases, between the cuticle and the epidermis and soon forms a sorus or pustule in which spores are produced.

The different kinds of spores that a species may possess vary in number from one to five. If all the spore forms in the life cycle are produced on one or a few closely related species of host plants, the rust is said to be **autoecious**. A large number of rusts produce their different spore forms on two unrelated sets of host plants. Such rusts are said to be **heteroecious**.

The different spore forms that may be present are unlike in form, have distinct names, and are produced in different ways. The names of the spores and the structures in which they are produced are as follows: **pycniospores**, or **spermatia**, produced in structures called **pycnia**, or **spermogonia**; **aeciospores**, or spring spores, produced in cup-like structures called **aecia** (singular **aecium**), or cluster cups; **uredospores**, or summer spores, produced in pustules known as **uredinia**; **teliospores**, or winter spores, in pustules known as **telia**; and a fifth kind originating from the teliospores and termed **basidiospores**.

Not all of these different spore forms are present in every species of rust. Any or all of them may be missing except the telial and the basidiospore stages. The telial stage is most frequently a resting stage. When a teliospore germinates, each of its cells produces a short germ tube, the basidium, which becomes transversely four-celled, each cell producing a basidiospore (Fig. 198, *E*). The other spores, with the exception of the pycniospores, germinate in the usual way, producing an extensive mycelium.

With such a large number of spore forms and often more than one kind of host involved, the completion of our knowledge of the life cycles of these plants has been a very difficult yet attractive problem. In this work, one kind of spore must be inoculated into or sown upon that plant believed to be its other or "alternate" host. If the inoculation results in infection, then the problem is at least in part solved, although further sowings on other related host plants are often necessary to determine its entire host range. The fungus must also be under observation constantly to detect which of the five possible spore stages it may possess on all these hosts. Eventually, after many such cultures and observations have been made, the facts are

fitted together to give the complete life history of the fungus. The details of this work will be better appreciated after the student has studied some of the rusts in more detail.

Life Histories of Important Economic Species. 1. *Stem Rust of Wheat* (*Puccinia graminis*). Wheat rust, or more properly the black stem rust of wheat, is, economically, one of the most important plant diseases known. Its absence some years and its great severity in other years are usually coupled with certain environmental factors of moisture and temperature,

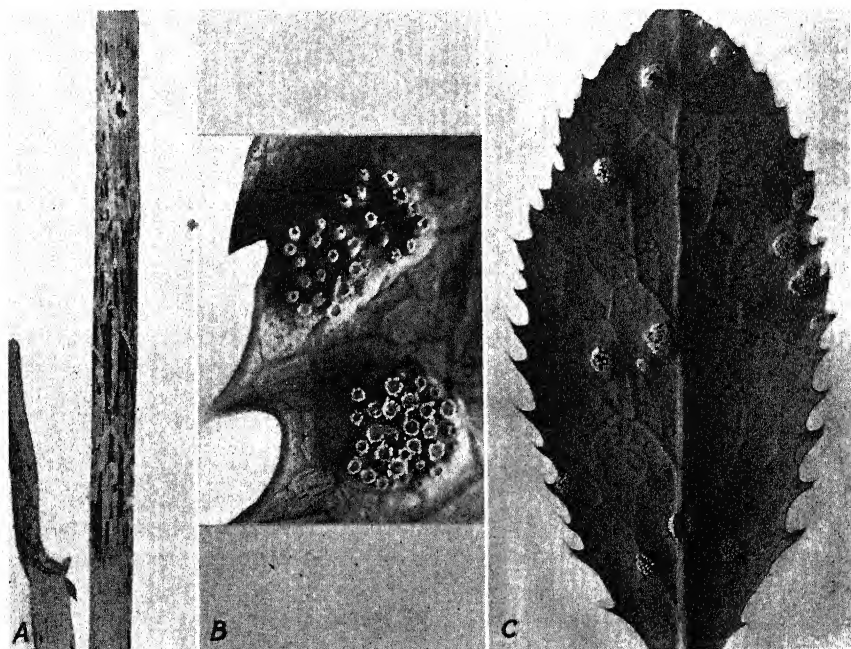


FIG. 197. *Puccinia graminis*, black stem rust of wheat. A, telial stage on stem of wheat; B, enlarged photograph of two aecial pustules on lower surface of barberry leaf; C, barberry leaf enlarged to show aecial pustules on lower surface.

and this has given rise to the idea that these factors are the direct cause of the rust disease. Such is not the case, but the fungus finds in a warm humid climate its best conditions for growth and hence virtual epidemics of the rust result, with disastrous effects on the wheat crop.

This rust is a heteroecious species producing certain of its spore stages on the leaves of the wild barberry plant and others on the wheat plant. In the spring of the year, perhaps in May, there appear on the upper leaf surfaces of the barberry plant small yellow or reddish spots, slightly raised above the surface of the leaf. These spots denote the presence of

the mycelium of the rust fungus, and the colored spots themselves are due to the diseased host cells parasitized by this mycelium. Each such spot on the barberry leaf contains small flask-shaped or conical structures (Fig. 198, *A*) formed of fungus mycelium. These are the **pycnia**. From small hyphae that line the inside of each pycnium, small spores, the **pycniospores**, are cut off. These spores were formerly regarded as not important in the life history of the fungus. This stage is followed, in the course of several days, by the aecial stage arising from the same mycelium which produced the pycnia. The **aecia** appear on the lower surface of the leaf in small discolored areas and consist, at maturity, of small open cups immersed in the tissue of the leaf (Fig. 197, *B, C*), breaking out through the epidermis. By this means they release the bright-orange or yellow **aeciospores** that are produced in chains from the bottom of the cup (Figs. 197; 198, *B*). These cups, because of their grouping, are also known as "cluster cups." The spores they carry are not able to reinfect the barberry leaf; but if one of them chances to fall on a suitable portion of the wheat plant, it will produce a germ tube that may enter the tissue of the wheat through a stoma and so start the infection of that plant.

After the lapse of about two weeks, a third spore stage, the **uredinium**, is formed on the wheat plant by the massing of the mycelium in definite spots below the epidermis. From the tips of special hyphae in this structure, there are cut off one-celled spores, the **uredospores** (Fig. 198, *C*). These gradually push up the epidermis until it bursts and the spores are disseminated. Uredospores are one-celled, rough-walled, and orange-brown or reddish in color. Consequently, this stage has come to be known as the "red rust" of wheat. The spores produced in this stage spread the disease to other wheat plants. It is at this stage that weather conditions determine whether or not there is to be a severe epidemic of wheat rust. If there has been a very light infection of wheat from the barberry or if weather conditions are unfavorable for the germination of the uredospores, the further progress of the rust will be retarded. But if infection from the barberry has been heavy, owing to the close proximity of barberry bushes to the wheat field, and if conditions are favorable for the distribution and germination of the uredospores, the resulting spread will be facilitated and an epidemic may result. Other wheat plants become infected by the uredospores, and in the course of 10 days or 2 weeks a new crop of uredospores is formed that may repeat the same stage. Consequently, these uredospores are often spoken of as "repeating spores." They are not capable of infecting the barberry.

Within a short time, further formation of uredospores ceases, probably partly as a response to the maturing condition of the host, and from the mycelium that has been producing uredospores, or from mycelia originating

from uredospores, a fourth kind of spore, the **teliospore**, is formed. These are heavy-walled, two-celled spores on a conspicuous stalk or pedicel (Fig. 198, *D*) and are dark brown or, in mass, black. This stage has been designated the "black-rust" stage. It appears on the wheat stalk as

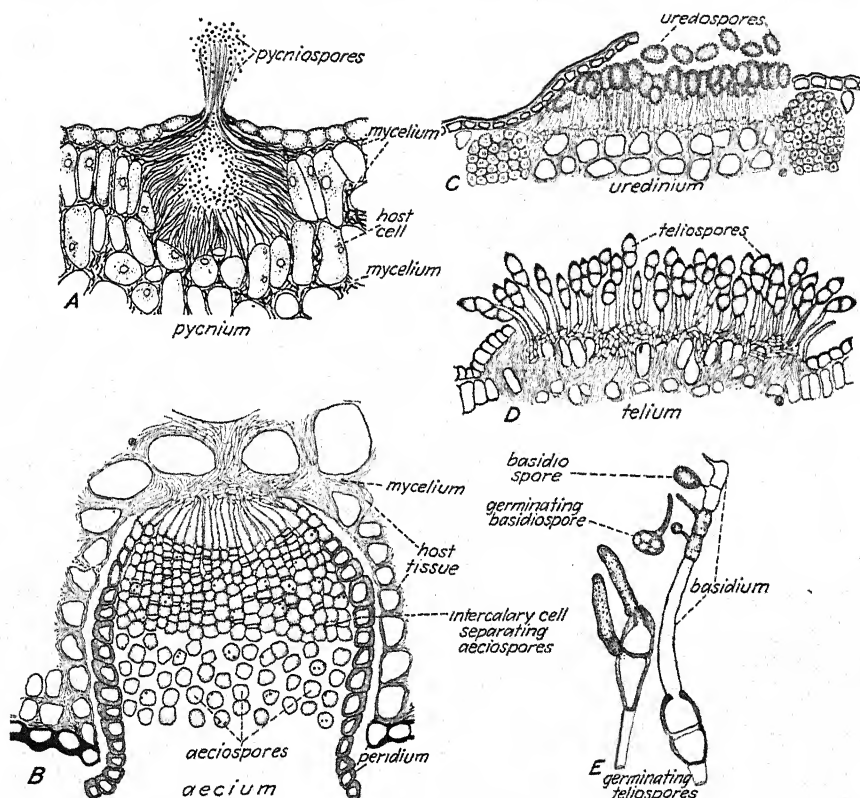


FIG. 198. *Puccinia graminis*. A, section through a pycnium; B, section through an aecium imbedded in the tissue of a barberry leaf; C, section through a uredinial sorus, with the one-celled, rough-walled uredospores borne on slender stalks that arise from a subepidermal mycelial complex; D, section through a telial sorus showing the two-celled teliospores on long pedicels arising from an internal mycelial complex; E, germinating teliospores; left, both cells of the spore germinating; right, only the apical cell germinating; the germ tube has been transformed into a basidium, from each cell of which a basidiospore has been or is being formed.

narrow black areas called **sori**, bursting through the epidermal layers (Fig. 197, *A*). By this time the wheat plant is mature, and further growth of the fungus is stopped. The teliospores are, therefore, resting spores and tide the fungus over the winter, remaining in place on the wheat stalk in the field or in the stack.

With the return of warm weather and warm rains in April or May of the next spring, these spores germinate. Each cell of the spore sends out a short club-like hypha which becomes divided into four cells (Fig. 198, *E*). This hypha is the **basidium**, and from each of its cells a small stalk is put out on which is borne a single spore, the **basidiospore**. These are wind disseminated, but it is not possible for them to infect a wheat plant. If one chances to alight on the leaf of a barberry, the germ tube that it produces may enter the leaf tissue and, after a short period of growth, the mycelium masses beneath the epidermis to form the pycnia already described (Fig. 199).

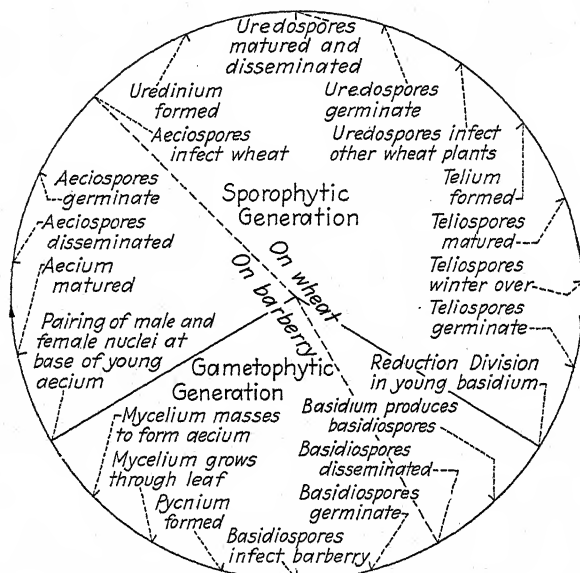


FIG. 199. Life-cycle diagram of *Puccinia graminis*.

As is the case with most plant parasites, adequate methods of control are based on a knowledge of the life history of the attacking organism. In northern climates, the black stem rust of wheat cannot perpetuate itself more than a single season without both the barberry and the wheat plants. Consequently, if either of these hosts is removed from the locality, the control of the disease is accomplished. It is a well-known fact, based on many observations and experiments, that where the wild barberry grows in profusion near a wheat field an epidemic of rust is likely to occur, its severity being dependent upon climatic conditions; likewise the removal of the barberry aids in eradication of the disease. There is some evidence to indicate that in portions of southern Texas the winters are mild enough to

allow the uredospores to winter over in viable condition and so reinfect the wheat again the next spring. If this is true, the barberry is not necessary in the life cycle in that region. Furthermore, some of the uredospores are sometimes carried by the wind to states farther north where they are able to infect wheat. Even though this may be true, it is still advantageous to destroy the common barberry, because in so doing, we tend to reduce hybridization of the rust and the production of new strains which are able to infect varieties of wheat resistant to established strains.

2. *Apple-cedar Rust*. Another rust (*Gymnosporangium Juniperi-virginianae*) of considerable economic importance attacks the leaves and fruits of the apple. This is also a heteroecious rust producing on the apple its pyrenial and aecial stages, and on the red cedar or juniper its telial stage. No uredinial stage is present in the life cycle. The stages on the apple are somewhat similar in appearance to the same stages in the wheat rust (Fig. 200, *B*). In the telial stage on the cedar, conspicuous rounded galls, 1 to 5 cm. diameter, are formed that are known as "cedar apples." In late April or May, following warm rains, there appear on the surfaces of these galls horn-like outward growths (Fig. 200, *A*) of a jelly-like consistency, in which are embedded the teliospores. These produce the basidia and the basidiospores, and the latter carry the fungus to the apple. Here again both host plants are essential for the completion of the life cycle, and the disease on the apple is easily controlled by removal of all cedars from the neighborhood of the orchard, particularly from the side toward the prevailing winds.

3. *White-pine Blister Rust*. Of recent years a rust known as a blister rust (*Cronartium ribicola*) of the white pine has become serious. Introduced from Europe, probably prior to 1900, it has spread over all of the northeastern United States—a region that has always produced the most and the best of the white pine. It is now present on related pines in our Western forests and in British Columbia and threatens the extinction of all the white pines. It is a heteroecious rust that produces aecia and pyrenia on the white pine and uredinia and telia on the leaves of currants and gooseberries, both wild and cultivated species (Fig. 200, *C-E*). The method of control consists in the eradication of the last two hosts from the neighborhood of white-pine plantations or forests. This is being done on a large scale in the best of the white-pine regions. The cost of keeping such areas free from gooseberries and currants for the duration of the rotation is said to be 4 to 15 cents per acre per year.

A large number of other rusts is of considerable economic importance. All of our cereal plants have one or more such diseases. They attack our forage crops such as clover and timothy; our fruit crops including apples, pears, peaches, and quinces are often parasitized by them; on our ornamental plants such as carnations, hollyhocks, chrysanthemums, and roses they are not uncommon; beans and asparagus are attacked by rusts in our gardens; and in the forest they are present on willows, poplars, pines, hemlocks, firs, and spruces.

Sexuality and Alternation of Generations. Nothing has been said so far concerning sexual reproduction in these fungi, and until about 1904 it was believed that none existed anywhere in the rusts. In 1904, it was discovered that, in the initial development of a young aecium, certain cells lying side by side became binucleated. There is no nuclear fusion at this stage, but the two nuclei remain paired in the cells. Although intensive researches were directed toward the problem, nothing could be discovered as to the origin of these two nuclei, and it was very generally believed that

the cells in which they occurred were ordinary vegetative cells, but that their nuclei had become slightly sexually differentiated, and the binucleated condition resulted from the conjugation of two of these cells.

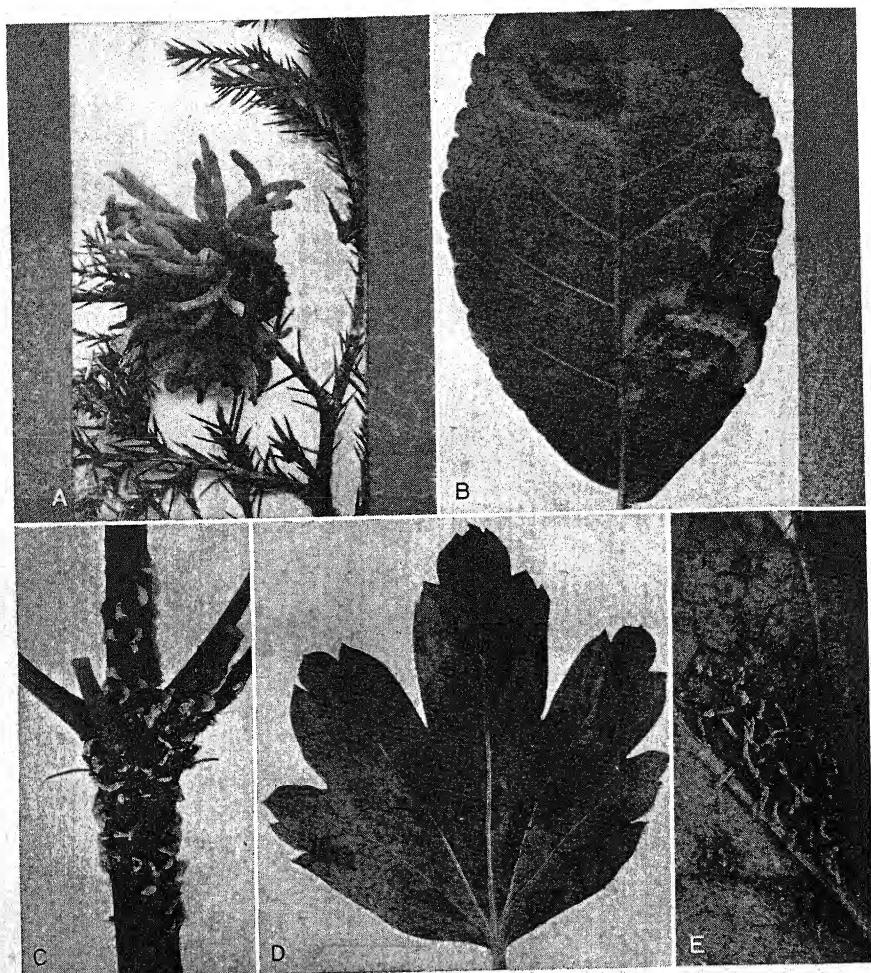


FIG. 200. A-B, apple-cedar rust. A, a "cedar apple" on juniper. This is their appearance in April or May, when the telial horns bearing the teliospores are prominent. B, apple leaf, lower surface view, showing the aecial stage. C-E, white-pine blister rust; C, aecial stage on main stem of seedling white pine; the orange bladdery pustules are a conspicuous feature of the disease on white pine in May; D, telial stage on lower surface of wild gooseberry leaf; the telial columns appear as brown hairs, as shown in the enlarged photograph in E.

For many years it has been a common conception that the pycniospores of rusts performed no function in the life cycle. Some regarded them as an asexual type of spore that had lost the ability to propagate the species and perhaps was gradually being dropped from the life cycle. Others believed them to be degenerate male

gametes that had long since ceased to take an active part in the sexuality of the species. One or the other of these views seemed to be necessary, because many experiments had failed to demonstrate that these bodies ever functioned in any way. New evidence has now been uncovered which indicates that not only are they male cells but that, at least in some species, the contained nucleus may be a functional gamete nucleus. After the pycniospores have been discharged from the pycnium, they come into contact with the tips of special hyphae that protrude in clusters through the stomata of the leaf near the pycnium. Each pycniospore nucleus dissolves its way through the wall into the cavity of the terminal cell of one of these hyphae. From there they migrate down the hyphae, passing through cell walls from cell to cell. They have not been followed through all their course, but eventually they are presumed to be the nuclei which become associated with the nuclei in other hyphal cells at the base of the young aecium, thus originating the binucleate condition found in that region. On the other hand, until the progress of these nuclei can be more definitely traced in their passage, it is not safe to draw conclusions. Even though they enter the cells of these special protruding hyphae, they still might never reach the region of the base of the aecium. Similar occurrences are known in certain Ascomycete fungi.

The binucleate cells lying at the base of the young aecium then proceed to form chains of spores that round up and become the aeciospores. As each spore cell is being formed, the two nuclei of the parent cell divide, the new spore thus receiving two nuclei, each of which is a descendant of one of the nuclei in the cells that fused. Consequently, the aeciospores are binucleate. Likewise, the teliospores are at first binucleate. At some time prior to germination of the teliospores these two nuclei fuse. This fusion is regarded as the culmination of the sexual process begun in the cells at the base of the aecium and is, therefore, the equivalent of a fertilization. Upon germination each cell of the teliospore produces a short hypha consisting usually of four cells (Fig. 198, *E*). This structure is the basidium. One of the divisions of the fusion nucleus to form the four nuclei for the four cells of the basidium is regarded as a reduction division to bring the chromosome number back to the $1N$ stage. Consequently, the usual interpretation placed upon these facts of the life history is that the binucleate stage, and likewise the fused condition of the nuclei in the teliospore, constitute the sporophytic ($2N$) part of the life cycle. The gametophytic stage is represented by the basidium, the basidiospores, the mycelium they form in the tissue of the barberry leaf, and the pycnium with its pycniospores up to the origin of the binucleate condition at the base of the aecium. If this is true, we have here a definite alternation of generations, different from that of most of the green algae in that the bulk of the plant is sporophytic instead of gametophytic. A somewhat similar condition was described for the smut fungi.

HIGHER BASIDIOMYCETES

General Characteristics. The group known under this name includes nearly all of the more prominent fungi such as mushrooms, toadstools, and puffballs. They differ from the preceding subclass in several particulars. They form more conspicuous fruiting bodies for the production of the spores. The basidia on which the spores are produced do not arise directly as a germ tube from a spore, as in the smut and the rust fungi, but are the modified terminal cells of an extensive mycelium. In this character the basidium corresponds to the ascus of the Ascomycetes but produces its spores externally rather than internally. Also, there is no such variety of

spores produced within this group as occurs in the rust fungi. Probably in most cases the basidiospore is the only type of spore produced, although conidia and chlamydospores are not unknown. Furthermore, the basidia on which the basidiospores are produced are usually grouped into a definite hymenial layer (Fig. 202, A). While rusts and smuts are parasitic, the higher Basidiomycetes are more uniformly saprophytic. In the proper season, they are likely to be found wherever there is a substratum rich enough in organic materials to support them.

The mycelium of these fungi is usually widely dispersed within the substratum and in many cases is perennial. Frequently it shows peculiar

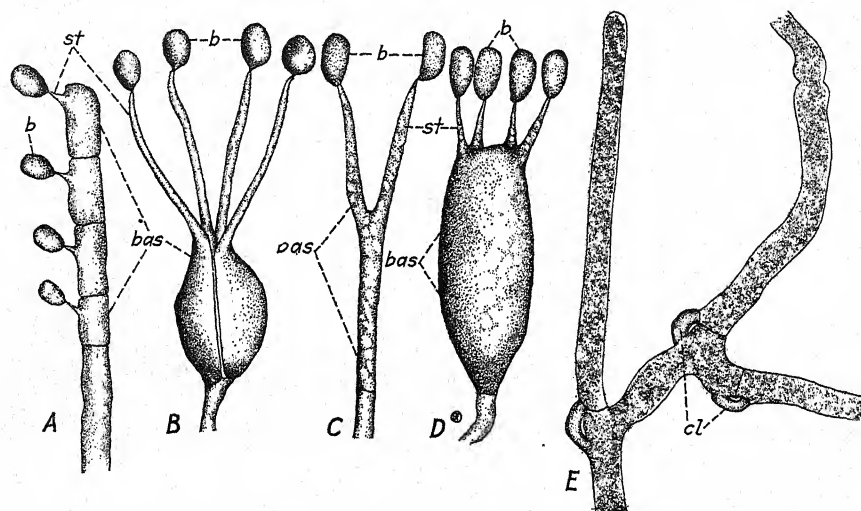


FIG. 201. Basidia and mycelium of higher Basidiomycetes. A, a cylindric four-celled basidium; B, longitudinally septate basidium; C, one-celled and two-spored basidium; D, one-celled and four-spored basidium; E, typical mycelium with clamp connections, *cl*; *bas*, basidium; *b*, basidiospores; *st*, sterigmata.

and characteristic structures known as **clamp connections** at the cross walls (Fig. 201, E). Arising from the germination of a spore, the mycelium eventually produces a sporophore that produces spores, and apparently the life cycle in most cases is not more complicated than this. Sporophores are initiated by the same sort of process that in the rust fungi gives rise to sori or pustules, *viz.*, the massing of the mycelium at definite points near the surface of the substratum. This mass of hyphae gradually takes on a definite form and emerges to the surface of the substratum. Further development depends upon the type of sporophore that is to be produced.

The simplest type of sporophore is shown by the lower members of the group, where it is a flat or more or less cushion-shaped body formed by

the massing of the mycelium on the external surface of the substratum (Fig. 204, *G, H*). In such a sporophore the hymenium is likely to be spread over the entire free surface of the sporophore. A further stage in the evolution of the sporophore shows the hyphae to have grown out in a more horizontal plane from the substratum, producing a shelf-like or bracket-like sporophore with the hymenium restricted to the lower and better protected surface (Figs. 204, *I*; 205, *C*). Further specialization consists in the production of a stalk or stem (Figs. 204, *A, D-F*; 205, *A, B, D*) which elevates the spore-producing portion above the general level of the substratum and results in a better distribution of the spores. The common mushroom is an example of this development. A second and entirely distinct line of evolutionary development, giving the maximum protection to the spores, is shown in development of the puffball type of sporophore (Fig. 204, *B*), in which the spores are protected until they are entirely mature and are set free by the collapse of the surrounding protective tissue.

The basidia produced by these sporophores are not of a uniform type. In one small family they are transversely septate (Fig. 201, *A*), showing relationship with the rusts and smuts; in another they are longitudinally septate (Fig. 201, *B*); but in most of the species they are one-celled (Fig. 201, *C, D*), usually producing four basidiospores on as many short, apically situated stalks, the sterigmata. The type of basidium produced is used as a basis for separating the subclass into orders. Morphologically, distinct bodies under the name of paraphyses rarely occur with the basidia, most of the elements that have gone under that name being only immature basidia.

Sexuality in the Higher Basidiomycetes. Definite sex organs are not present in any species of this group; yet there has been developed what may be looked upon as the equivalent of the sexual process. The cells of the mycelium that is produced by the germination of a spore eventually become binucleate. Apparently, at times, this is accomplished through a fusion between two cells of adjacent hyphae, but variations of this method are known. As a result, the terminal cell of the hypha, like the terminal cell of the ascogenous hyphae of the Ascomycetes and like the teliospore of the rusts, is binucleate. This terminal cell (Fig. 202, *B*) becomes the basidium. In the young basidium the two nuclei fuse (Fig. 202, *C*). This fusion nucleus then divides twice to form four nuclei (Fig. 202, *D, E*). From the tip of the basidium, four (usually) minute tube-like processes, the young sterigmata, arise, and a small enlargement (Fig. 202, *E, F*) appears on the tip of each. Into each of these enlargements, there passes, through the hollow sterigma, a small amount of cytoplasm together with one of the nuclei from the basidium (Fig. 202, *F, G*). These terminal enlargements of the sterigmata become the spores. The fusion of the nuclei in the basidium

is regarded as the final step in the sexual process, and one of the two nuclear divisions that follows this fusion is believed to be a reduction division. If this is true, a condition similar to that which exists in the rusts is present here, and the sporophytic stage would include the binucleate mycelium and the young basidium up to the time of the reduction division.

Economic Importance. *Mushrooms.* Perhaps the greatest single feature of economic interest in connection with the higher Basidiomycetes is the growing of one or a few species on a commercial scale for use as food. France was long the center of this activity, marketing the product both in the fresh condition and canned for export. In the United States the mushrooms are mostly marketed in the fresh condition, but many are also

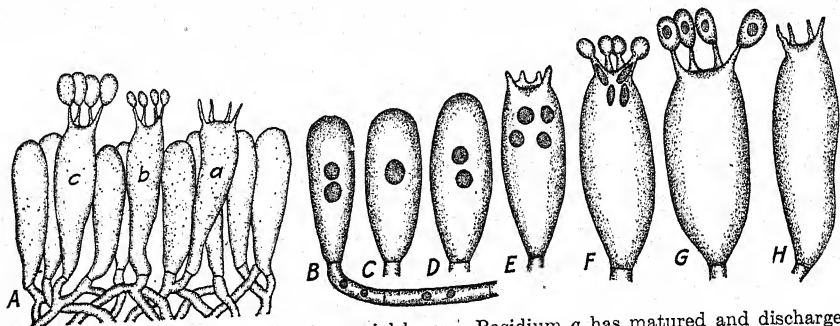


FIG. 202. A, small portion of a hymenial layer. Basidium *a* has matured and discharged its spores, leaving the four slender sterigmata; basidium *b* shows immature spores; basidium *c* shows four spores ready for discharge. The slightly smaller structures between the maturing basidia are immature basidia that may or may not produce spores. B, young binucleate basidia on the end of a hypha; C, basidium in which the two nuclei have fused; D, basidium again binucleate through the division of the fusion nucleus; E, a four-nucleate basidium, showing the beginning of sterigmata; F, basidium with the spores forming on the sterigmata and the beginning of nuclear migration through the sterigmata; G, basidium with nearly mature spores; H, basidium that has discharged its spores.

canned. The value of the Pennsylvania-grown product alone now varies from 20 million to 25 million dollars annually. Most of the American product is grown in the vicinity of the larger cities, such as New York, Philadelphia, Cleveland, Chicago, St. Louis, and Minneapolis.

In the United States, *Agaricus campestris* (Fig. 205, B) and perhaps two or three other related species grown in cultivation are practically the only ones to be found on the markets. *A. campestris* is itself a wild species and there are in the eastern United States more than 500 other wild species that are edible. There is no botanical distinction between mushrooms and toadstools, edible and poisonous species occurring in the same family and often in the same genus. There is no simple test that can be applied to determine whether they are edible or poisonous. The only way of distinguishing between them is to learn to recognize the different species. On the markets of the large European cities, as many as 50 or 60 different

species of wild mushrooms are for sale in their season, indicating a much more extensive and intimate acquaintance with these plants by the populace.

Tree Diseases and Timber Decays. As previously stated, most members of this group are saprophytes; yet in one way or another several kinds are able so to weaken their hosts, if in no other than a mechanical way, as to be of importance from an economic standpoint. Many species grow in the heartwood of living trees (Fig. 203, *B*), breaking down the original composition of the cell walls. This makes the tree more liable to be wind thrown and renders the wood useless for lumber. Every fruiting body growing on a tree or log is ample evidence of the presence of an abundant mycelium

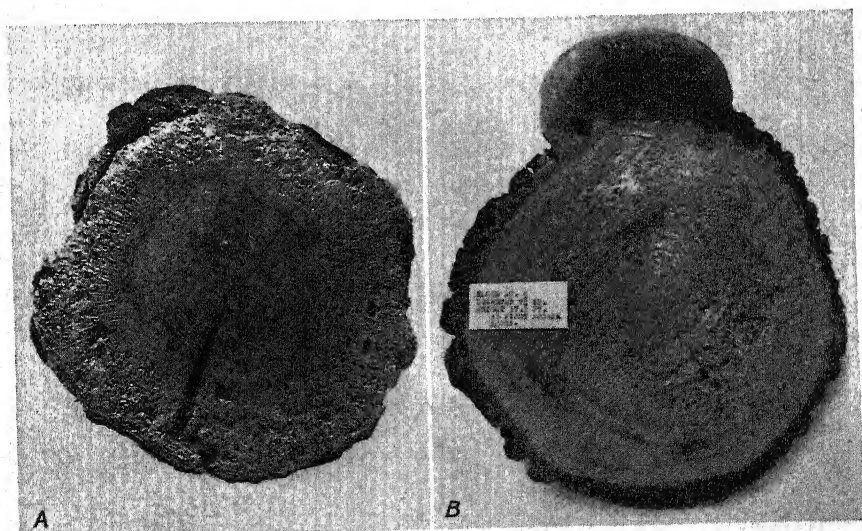


FIG. 203. Fungi and wood decay. *A*, a block of oak wood with the sapwood entirely decayed; *B*, a block of ash wood with the heartwood entirely decayed. The sporophore is shown on the upper side of the block.

within. Other agencies than fungi have little or no effect in causing timber to decay, as evidenced by the well-known fact that timber immersed in water or buried in the soil where the fungi cannot grow because of the lack of oxygen, or kept in a dry place where there is not enough moisture to support fungous life, will last almost indefinitely. This explains why fence posts and telegraph poles rot most at the surface of the ground, for it is at that point that there is a proper balance between moisture content and oxygen supply for the growth of the fungus. Likewise, a wood of high resin content does not decay because of the waterproofing effect of the resin. The same applies in part, at least, to the use of paint and varnish as well as to such wood preservatives as creosote, asphaltum, and other coal-tar

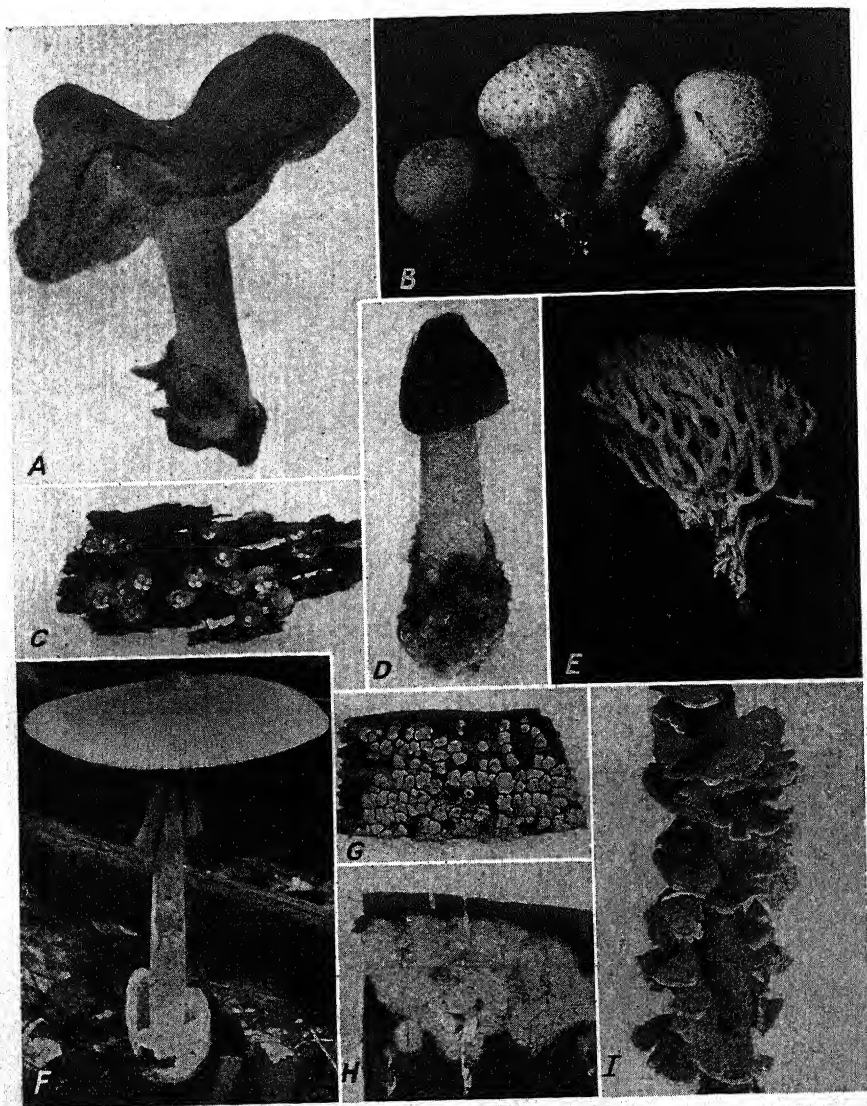


FIG. 204. Different kinds of higher Basidiomycetes. *A*, *Hydnum repandum* of the toothed fungi; *B*, *Lycoperdon gemmatum*, a puffball; *C*, *Crucibulum vulgare*, one of the bird's-nest fungi. The egg-like bodies in the cups contain the spores. *D*, *Dictyophora Raveneli*, a stinkhorn fungus; *E*, *Clavaria subcespitosa*, a coral fungus; *F*, *Amanita Caesarea*, a gill fungus showing the pendent membranous annulus and the well-developed volva at the base of the stem; *G*, *H*, types which do not form either pileus or stem but lie flat on the substratum and have a smooth hymenial surface; *I*, *Stereum rameale*, a pileate type with smooth lower surface.

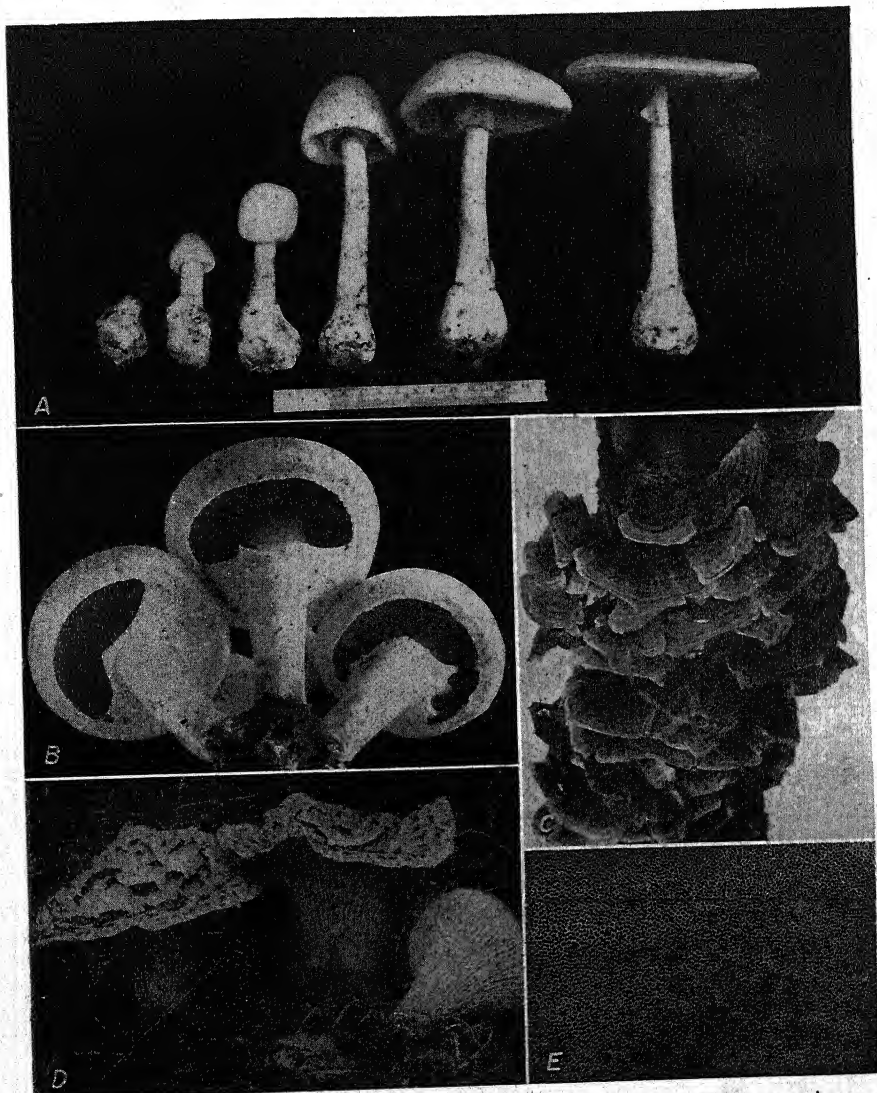


FIG. 205. Different kinds of higher Basidiomycetes. *A*, *Amanita phalloides*, a poisonous mushroom, showing the membranous annulus hanging on the stem under the pileus, and with a close-fitting volva at the base; *B*, *Agaricus campestris*, the common mushroom of commerce. Note the well-developed veil tearing away from the margin of the cap and remaining on the stem as an annulus. *C*, *Polyporus versicolor*, a common type of pore fungus; *D*, *Cantharellus floccosus*, a beautiful orange-colored mushroom with imperfectly developed gills; *E*, pore surface of *Polyporus versicolor* enlarged. The spores are produced within these pores.

products, although in these cases the substances contain elements that are actually toxic to the growth of the fungi.

These same wood-decaying organisms must be regarded also as a benefit to man. If it were not for them, the trees and the brush that fall in the forest would accumulate on the forest floor until the woods would be entirely impenetrable. At the same time, the decay continually adds new elements and compounds to the soil to be used over again.

Different Kinds of Higher Basidiomycetes. Probably the best known group of higher Basidiomycetes is that of the gill fungi (family Agaricaceae), which includes the bulk of those commonly known as mushrooms and toadstools, in which the sporophore usually consists of a stalk and cap (Figs. 204, *F*; 205, *A, B, D*), with the basidia covering the surfaces of leaf-like plates, or gills, on the lower surface of the cap. These gills vary in color in different species, the color being due to the color of the spores. Sometimes the gills are protected for some time previous to the maturity of the spores by a veil extending from the margin of the cap to the stem (Fig. 205, *B*). This veil breaks as the sporophore increases in size and may remain on the stem in the form of a distinct membrane, or **annulus** (Figs. 204, *F*; 205, *A, B*). In addition, there is sometimes a veil in which the entire sporophore is enclosed during the early stages of development, and this usually splits and allows the sporophore to emerge, itself remaining at the base of the stem as a cup, or **volva** (Figs. 204, *F*; 205, *A*). There are several hundred species in this group in the eastern United States, of which less than 25 are known to be poisonous. Most of the common poisonous species belong to the genus *Amanita*.

Another group (family Polyporaceae) contains the bulk of the more conspicuous shelf fungi or bracket fungi (Fig. 205, *C, E*), in which the basidia line numerous tubes that open downward in an even layer on the lower surface of the bracket. Some of this group are edible, but some are known to be poisonous, though most are of a tough or woody consistency. The special importance of the group lies in their ability to bring about timber decays.

The toothed fungi represent another family (Hydnaceae) in which the hymenium covers the surfaces of downward-projecting teeth or spines (Fig. 204, *A*). Few if any of this group are of such consistency as to render them edible. The coral fungi (family Clavariaceae), often with very beautiful and delicate fruit bodies (Fig. 204, *E*), belong also in this series.

Still other types of higher Basidiomycetes exist in the group of the puffballs (Fig. 204, *B*) in which the spores are retained internally until fully matured, when they can be forced out in the form of a fine dust or powder. One species, the giant puffball, sometimes reaches a diameter of more than 2 ft. All puffballs are edible, but they must be used before the flesh begins

to turn dark on the inside, when they sometimes develop a bitter taste. More closely allied to this group than to the preceding families are the peculiar bird's-nest fungi and the stinkhorns. The sporophore of the former is in the form of a cup or vase in which are contained small egg-like bodies which contain the spores (Fig. 204, *C*). In the stinkhorns the sporophore is typically a cylindrical body at the apex of which the spores are produced (Fig. 204, *D*). These fungi are readily recognized by their bizarre shapes and their peculiar and unpleasant odors. Neither they nor the bird's-nest fungi are desirable for food.

FUNGI IMPERFECTI (IMPERFECT FUNGI)

In addition to those species of fungi falling properly into the three main subclasses of the fungi, there exists a large number of species the life histories of which are in doubt, but which are not known to possess the characteristics that would place them in either of the three previously described subclasses. Some of these consist only, so far as known, of sterile mycelium, but in most of them asexual spores entirely comparable with those (conidia) produced by many of the Ascomycetes are present. A few such species, previously referred to this group, are now known to be conidial stages of Basidiomycetes, and many more to be similar stages in the life history of Ascomycetes. Perhaps some have lost all connection with other stages, reproducing entirely by asexual means. The life histories, so far as known, are, therefore, quite simple. The different methods of producing spores are shown in Fig. 182.

The majority of the species of the group are saprophytes; yet large numbers are parasitic, particularly on the leaves and fruits of plants, and some are of great economic importance. Because of their importance, many species previously referred to this group have been quite thoroughly studied and now are known to be asexual stages of Ascomycetes and are so classified. In case of parasitic leaf-inhabiting species, heavy infection, with the consequent consumption of elaborated foods and the destruction of considerable amounts of photosynthetic tissue, represents a severe drain on the vitality of the host plant. Others cause the formation of definite cankers on limbs and branches or of spots or rots on fruits, much of which can be avoided by the correct use of fungicidal sprays such as Bordeaux mixture and lime sulfur. Still others cause degradation of fabrics. Many of the saprophytic forms are among the important soil organisms.

CHAPTER 16

BRYOPHYTA—LIVERWORTS AND MOSSES

GENERAL CHARACTERISTICS

The division Bryophyta or bryophytes is a small group of terrestrial plants numbering 20,000 to 25,000 species. As a group, they have world-wide distribution, occurring in all climates of the earth from the tropics to the subarctic and subantarctic regions, wherever there is moisture enough to sustain plant life. While the bryophytes are regarded as terrestrial plants, as distinguished from the algae, which are an aquatic group, the range of habitat is diverse. At one extreme, they grow in situations where they are almost constantly submerged in water; at the other, on dry rocks, where the soil is scant and moisture occasional. They are also found in all situations between these extremes. In general, however, the plants can be said to occur in moist situations, as on damp rocks in ravines, on sheltered cliffs and moist soil, and on decaying logs in forests.

The Plant Body. The plant body of the members of the bryophytes is small, attaining in the largest specimens a length of but a few inches. Like that of the thallophytes, the plant body is a thallus; yet the thallus of the bryophytes shows remarkable advances over that of most of the algae. The plant usually grows attached to the soil or other substratum by organs known as **rhizoids**, which are single-celled or multicellular, filamentous structures, the single-celled ones resembling the root hairs of higher plants. The lowest type of bryophyte plant body is an expanded structure, several to many cells thick, which lies flat on the substratum. In many of the higher bryophytes, there is differentiation into a stem-like portion and expanded leaf-like structures. These organs however, lack the characteristic vascular tissue of stems and leaves. The bryophyte plant body is regarded merely as a highly differentiated thallus (Fig. 206).

The Alternation of Generations. The characteristic alternating gametophytic and sporophytic phases which originated in the algae are firmly established in the bryophytes. The sporophytic phase is much more highly developed than in most of the algae and considerable variation in the size, structure, and relative importance of the sporophytic structure is found in the bryophytes. In the lower orders, the sporophyte is a simple structure with little differentiation of tissues, while in the higher orders the sporophytic structures are more highly developed, with greater dif-

ferentiation of tissues. The sporophyte is always dependent upon the gametophytic structures for at least a portion of its food materials. While the sporophytic phase in general shows an advance over that in the algae, it is the gametophytic phase of the bryophytes that still remains the conspicuous one. The gametophyte, though small, is highly developed and differentiated and has become well adapted to the terrestrial habitat. The gametophyte is the independent structure in the life history. It is attached to the soil and always supplies at least the moisture and the mineral food materials from its tissues to the dependent sporophytic structures. The gametophytic structures not only are highly efficient from a physiological standpoint but show remarkable development in the matter of asexual reproduction. Many of the bryophytes have developed such efficient methods of asexual reproduction that they approach independence of sexual reproduction as a means of increase and distribution. The point should be emphasized that the bryophytes are the group in which gametophytic supremacy has been attained. This supremacy is expressed in the highly developed and well-differentiated gametophytic structures (thallus) with adaptations for the terrestrial or land habit, in the physiologically efficient structures, and in the variety and efficiency of the asexual methods of reproduction.

Classification. The Bryophyta constitute one of the great divisions of plants. They differ from the algae and fungi in numerous structural and reproductive features. Although many of the marine algae show differentiation of tissues and structural complexities, the bryophytes have developed these features to a higher degree than most of the algae. The production of **multicellular sex organs, antheridia and archegonia**, during the gametophytic phase of the Bryophyta is a higher development than is shown by any member of the Thallophyta. The capsule, or spore case, of the moss sporophyte with its complex differentiation of tissues and



FIG. 206. *Conocephalus*, showing habit of growth on rock.

elaborate mechanism of dehiscence also is a structural advance over the algae and fungi.

The Bryophyta are divided into two classes each of which is further subdivided into three orders. The general scheme of classification is as follows:

Class 1. Hepaticae, or liverworts.

Order 1. *Marchantiales*, or thallose liverworts.

Order 2. *Jungermanniales*, or leafy liverworts.

Order 3. *Anthocerotales*, or horned liverworts.

Class 2. Musci, or mosses.

Order 1. *Sphagnales*, or bog or peat mosses.

Order 2. *Andreaeales*, or rock mosses.

Order 3. *Bryales*, or true mosses.

HEPATICAE—LIVERWORTS

GENERAL CHARACTERISTICS

The hepatics or liverworts are the lowest of the Bryophyta. They are found inhabiting damp or wet situations to a much greater extent than are the mosses, but only in rare cases are they entirely aquatic. The plant body is always prostrate, or practically so, and varies from a flat, dichotomously branched structure in the thallose hepatics to a plant with creeping stem and leaf-like expansions in the so-called "leafy liverworts." In all forms, however, including even the leafy types, the symmetry is distinctly dorsiventral; *i.e.*, there is a distinct upper or dorsal surface and a distinct ventral or lower surface. This is in contrast to the radial symmetry of mosses. Rhizoids are developed on the lower surface of the plant, except in those few cases where the plant is aquatic. These rhizoids are always unicellular structures, another point of contrast to mosses which have rhizoids with cross walls. No more than a faint trace of conducting system is present in the liverworts, and that only in the highest developed species.

The sex organs are either embedded in the dorsal tissue of the plant or are produced on special branches known as the **gametophores**. Following fertilization of the egg, there is developed a sporophytic body which varies in complexity but is always attached to the gametophyte and, except in the best developed species, is entirely devoid of chlorophyll and, therefore, is dependent upon the gametophyte for its food. In the lowest forms, the sporophyte consists mostly of sporogenous tissue, but within the group there occurs a progressive sterilization of potentially sporogenous tissues, until in the highest forms the spores arise only from a limited amount of tissue, the remainder either assisting in the nutrition of the spore-producing cells or aiding in the dissemination of the spores.

The liverworts have numerous methods of vegetative multiplication. Fragmentation of the branching thallus may occur in most species. Buds of simple, though multicellular, structure are frequently formed among liverworts. These buds are produced on the gametophytic structures and, although differing structurally from the single-celled spores formed in the algae and fungi, they serve the same purpose. They are a means by which a plant may be multiplied during its vegetative stage.

ORDER I. MARCHANTIALES.—THALLOSE LIVERWORTS

The order Marchantiales constitutes a group of widely distributed plants generally inhabiting moist locations. Some species, however, grow in exposed situations that are dry at certain seasons of the year although moist at others. Liverworts usually develop a flat, branching thallus, or gametophyte, 1 to 4 in. long, and often with conspicuous lobes. Because of the fancied resemblance of the thallus to the mammalian liver, these plants have been called liverworts, or liver plants. The Marchantiales show variation in size and structural development of the thalli. They are usually simple in form and structure with very little cell differentiation. In others, the thallus is differentiated into an epidermis, chlorophyll-bearing cells, and possibly some storage tissue. Although not universally found, air chambers in the thallus may be present and often are well developed with pores in the epidermis that function in the exchange of gases, especially oxygen and carbon dioxide.

The sporophyte of the Marchantiales is a small inconspicuous body that is relatively simple in structure. Within the group, sporophytes vary in size and differentiation of tissue. While the sporophytes of the Marchantiales show an advance over those of green algae, they still are relatively simple structures. Higher development is attained in other orders of the Bryophyta.

Marchantia and Related Forms—Family Marchantiaceae. The members of this family are terrestrial plants of thallose form. The flat, lobed thallus growing prostrate, with the ventral side attached to the substratum, is one of the characteristics of this group of liverworts. The gametangia are generally produced on gametophores, highly modified branches of the thalli, usually differentiated as to sex. In the related plants that do not have gametophores, the sex organs are developed in groups on slightly raised portions of the thalli.

The members of the family Marchantiaceae differ from other liverworts in the structural development of the sporophyte. A well-developed **foot**, a short **stalk**, and a **capsule** with **elaters**, produced among the sporeforming cells, or **sporocytes**, characterize the sporophyte of the Marchantiaceae.

The Gametophytic Phase. The gametophytic phase has its origin in the

maturation of the spores. The spores are the first structures of the gametophyte. Upon germination, each spore develops a germ tube, a short filament of cells which, by growth from an apical cell, soon broadens out into the thallus.

The thallus is a dichotomously branched structure with dorsiventral symmetry. It increases in size by growth from one or more apical cells. The apex of each branch of the thallus is more or less notched and at the base of each notch an apical cell is located. In *Marchantia* the mature thallus attains a length of 2 or 3 in., and in other genera of the Marchantiaceae it may be even larger. Rhizoids attach the thallus to the substratum. These are single-celled, hair-like structures that originate from

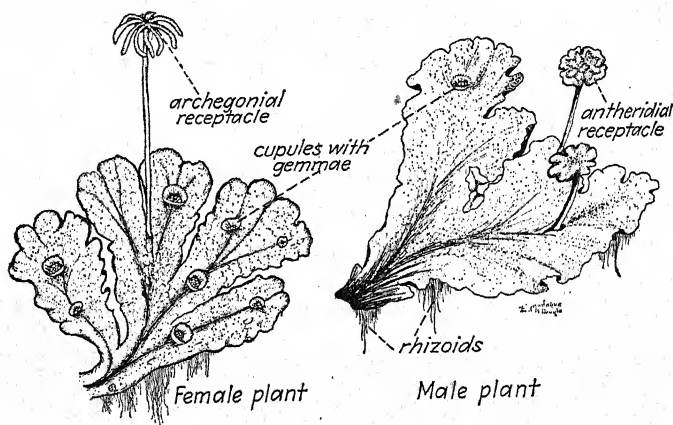


FIG. 207. Male and female plants of *Marchantia*, both showing cupules with gemmae and rhizoids. (Drawings by Edna S. Fox and Elsie M. McDougale.)

the outer cells of the lower surface of the thallus. In many of these structures the inner surface of the wall is smooth, but in others it is roughened by wart-like or finger-like projections into the cell cavity. These projections may even extend nearly across the cavity, but they are never complete partitions. Thin leaf-like scales also occur, on the underside of the thallus, particularly along the midrib (Fig. 207).

The upper part of the thallus is covered by a layer of well-defined epidermal cells, which usually contain chlorophyll, and is provided with pores or openings. Each pore is surrounded by a group of modified epidermal cells. The number and arrangement of these cells vary considerably in the different genera of the family (Fig. 208). In some they are almost suppressed, while in others there is an elaborate equipment of these cells. The genus *Marchantia* occupies an intermediate position in this respect, having several tiers of these cells arranged in the form of a

definite chimney. Although these cells may be called guard cells, seldom do they regulate the opening of the pores.

Internally, the thallus body is divided into two regions. The lower half or more of the thallus consists of compactly arranged, thin-walled parenchyma cells which probably serve as storage cells. These cells have little chlorophyll. The space between this region and the upper epidermal layer is divided into definite compartments separated by erect columns of cells supporting the epidermis. Each compartment opens to the outside through a single pore described above. Within these compartments are produced loosely arranged chlorophyll-containing cells. In *Marchantia*

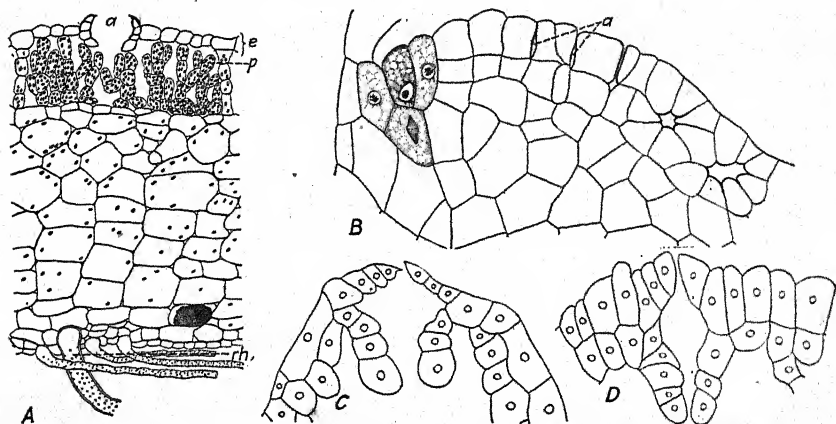


FIG. 208. Structural features of the thallus of members of the Marchantiales. A, cross section through thallus of *Marchantia*; a, opening of air pore; e, epidermis; p, plastids; rh, rhizoids; B, apical region of an archegonial head, showing origin of air chambers, a; C, and D, air pores; C in *Fimbriaria* and D in *Plagiochasma*.

these cells are in the form of branched filaments originating from the floor of these cavities. The loose arrangement of these cells and the presence of pores facilitate gaseous exchange for respiration and photosynthesis (Fig. 208, A).

Asexual multiplication may occur by fragmentation. The growing tips of the branching thalli continue development, while the central, basal portion decays, finally separating the branches. In certain genera, as in *Marchantia* and *Lunularia*, special asexual reproductive bodies called gemmae are produced. These **gemmae**, or buds, are formed in small **cupules** on the upper surface of the thallus (Fig. 207). Some investigators believe that these cupules are in reality specialized air chambers. Each cupule has an elevated margin and the buds, or gemmae, are produced on short stalks attached to the bottom of the cupule. The gemmae originate

from single cells arising from the superficial layer of the bottom of the cupule. By a series of transverse walls, followed by vertical walls, a thin plate-like structure is formed. The bud at maturity is a few layers of cells in thickness and notched on two opposite sides. In each notch there is found an apical cell which is capable of continuing the growth of the bud when it is suitably placed for growth. These buds are green in color and are held erect by their short stalks. When they fall on the soil, they grow into new thalli. This is a method of rapid multiplication.

Sexual Reproduction. A distinguishing feature of the members of the Marchantiaceae is the tendency to produce the sex organs in groups. In some genera of the Marchantiaceae, the sex organs are merely grouped on the thallus. In others, they are grouped in specialized structures called **receptacles**. The receptacles are, according to the genera, either sessile or stalked. The stalked receptacles are called **gametophores** (Fig. 207). A rather clearly defined evolutionary series of forms can be arranged from those forms which have the sex organs merely grouped on the thallus to those with stalked gametophores. Those genera having the more sessile arrangements are regarded as the lowest forms and those having the more highly specialized branches, other things being equal, the higher forms.

Marchantia produces highly specialized archegonial and antheridial gametophores which are produced on distinct thalli. The male and female plants may be distinguished by the characteristics of their gametophores. The gametophore consists of a stalk bearing an expanded, lobed, disk-like upper part, the receptacle. The receptacles are provided with several apical cells. In the archegonial receptacle, these are located between the long finger-like projections, and in the antheridial receptacle, in the notches of the margins of the characteristic disk. The sex organs are developed in each case from the segments of the apical cells produced on the upper or dorsal surface of the receptacle. The antheridia remain on the upper side, but in the female receptacle, the growing points are pushed underneath by the rapidly enlarging cells of the upper part of the structures, and therefore the archegonia are forced to the underside of the receptacle. The archegonia are protected from excessive evaporation by the presence of thin layers of protective tissues or scales hanging from the underside of the branches of the receptacles and covering the young archegonia. At maturity, the archegonia are pendulous on the underside of the receptacles.

The Sex Organs, or Gametangia. The sex organs, or gametangia, of the Marchantiales are essentially alike in all genera. Both antheridia and archegonia originate from superficial cells derived from segments of the apical cell near the tips of the thallus or, in the higher forms, near the growing points of modified branches (Fig. 208, B).

At maturity, the antheridium, or microgametangium, is an ovoid structure supported by a short multicellular stalk. In transverse section it appears circular. Structurally the antheridium consists of an outer wall of sterile cells and an inner fertile mass of small cubical cells known as the spermatogenous tissue (Figs. 209, A-G; 213, A). Each cell of this tissue divides diagonally forming two, and from each of these a minute

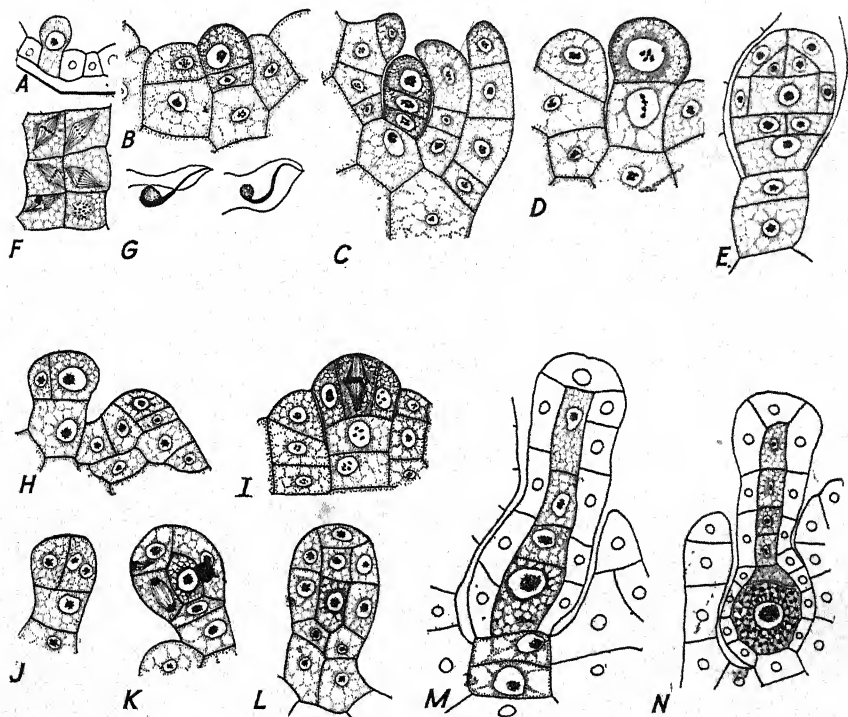


FIG. 209. Development of the sex organs of the Marchantiales. A-F, antheridia of *Riccia*; H-N, archegonia of *Marchantia*; A-E, young stages in antheridial development; F, final division to form the sperm cells; G, mature sperms; H-L, young stages in archegonial development; M, older archegonium; N, mature archegonium.

biciliate sperm, or microgamete, is developed. At maturity, the wall of the antheridium ruptures, and the sperms are free to swim to the archegonia. In *Marchantia* the antheridia are produced in large numbers, the older ones toward the center and the younger ones toward the margins of the disk-shaped receptacles. The surrounding vegetative tissue on the surface of the antheridial receptacle builds an overgrowth which makes the antheridia appear to occur in depressions.

At maturity, the archegonium, or macrogametangium, is a flask-shaped structure. It has an enlarged basal portion, the **venter**, a long **neck**,

and a short **stalk** attaching the organ to the thallus. The venter of the archegonium contains the **egg**, or **macrogamete**, and a **ventral canal cell**. The neck consists of a central row of cells, and the surrounding neck wall cells. The upper part of the neck is made up of specialized cap cells (Figs. 209, *H-N*; 213, *B*). Both venter and neck are circular in transverse section. When the archegonium is mature, the neck canal cells and the ventral cell disintegrate, the cap cells come off, and a canal is opened from the tip of the neck to the egg cell in the venter. The sperms move through the liquid formed from the disintegration of the neck canal cells.

Mature archegonia are frequently found in young receptacles before much elongation has occurred in the stalks of the gametophores. This location, together with the habitat of these plants, explains the ease with which the sperms reach the archegonia after their release from the antheridia. The liverworts all grow in situations where at times there is sufficient water to serve as a medium through which the sperms reach the eggs. Under greenhouse conditions, with just the ordinary "watering" of the plants, fertilization generally occurs.

Syngamy, or Fertilization. The sperms, or microgametes, may be attracted by chemicals given off by the archegonium. Frequently several of these microgametes penetrate the neck of the archegonium and reach the venter, but normally only one of them unites with the egg, or macrogamete (Figs. 209, *G*; 210, *A*). Each gamete carries the $1N$ number, or haploid complement, of 8 chromosomes. Their union brings the $2N$ number, or diploid complement, of 16 chromosomes into the nucleus of the zygote.

The Sporophytic Phase. Fertilization initiates the diploid phase of the life cycle. With union of gametes, the **zygote**, or *first cell of the sporophyte*, is formed. It also results in an activation or physiological stimulation that expresses itself in the growth and further development of that structure. Compared with the usual condition in most green algae, there is considerable development of diploid tissue following fertilization.

The development of the young sporophyte, sometimes called the **embryo**, proceeds from the growth of the single-celled zygote. The first division of the zygote is transverse to the vertical axis of the archegonium and the resulting cells give rise to different parts of the sporophyte. The outer of the two cells develops the capsule, containing the spore-bearing tissue, and the inner one forms the nutritive portions of the sporophyte, the foot and stalk. Further development of the embryo proceeds at first by mitotic divisions, which first form four and then eight cells. Later divisions produce cells in irregular formation. As the young embryo develops, it elongates vertically (Fig. 210).

The development of an embryo in the bryophytes and other plants

has been regarded by some botanists as an important evolutionary advance over the algae and fungi. This development has been made the basis for the establishment of a proposed new division, the **Embryophyta**, in the classification of plants. According to this scheme the Embryophyta include the bryophytes and all plants regarded as higher on the scale of evolution. While some botanists regard the Embryophyta as a valid division of the plant kingdom others think a division based on the development of the embryo has little significance. They point out that many thallophytes develop early stages that may also be called embryos and therefore cannot be excluded from the Embryophyta.

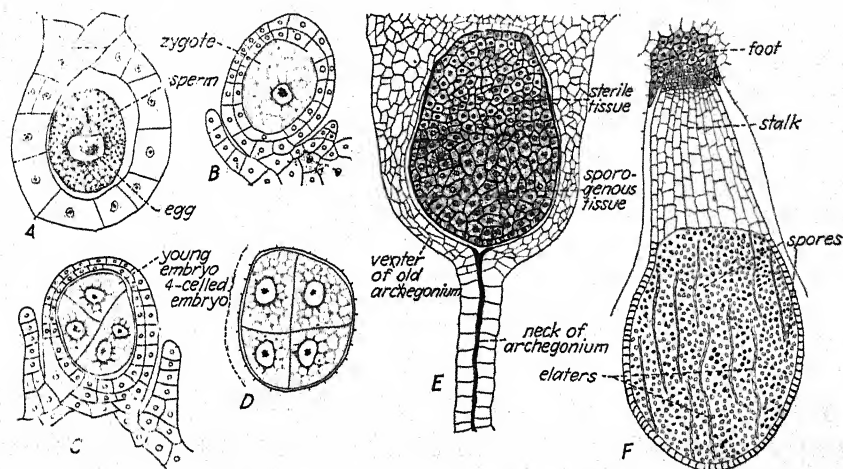


FIG. 210. Stages in development of sporophyte of *Marchantia*. A, fertilization of egg by sperm; B, young zygote; C and D, early stages in division of young sporophyte; E, multicellular sporophyte, showing differentiation of potential sporogenous and sterile tissue; F, mature sporophyte.

The sporophyte developing from the zygote is retained in the venter of the archegonium during its embryonic stages. The foot portion of the sporophyte is attached to the archegonial receptacle, and as the young sporophyte develops, the venter of the archegonium enlarges and for a considerable time entirely envelops the embryo. The old archegonium is at this stage called the **calyptra** (Fig. 210, E). Eventually, by elongation of the stalk, the capsule is pushed through the calyptra, which remains at the base, around the foot.

The Mature Sporophyte. The mature sporophyte is ellipsoid, only a few millimeters long. Structurally it consists of an expanded foot, a short, relatively thick stalk, and a spore case, or capsule. The sporophyte is pendulous from the female receptacle to which it is attached by the anchor-

like foot. The foot and stalk show only slight differentiation of tissues. The capsule contains the spore-bearing tissues and numerous sterile elongated cells, forming elaters. The tissues of the capsule are the most highly differentiated in the sporophyte. For a while, after emerging from

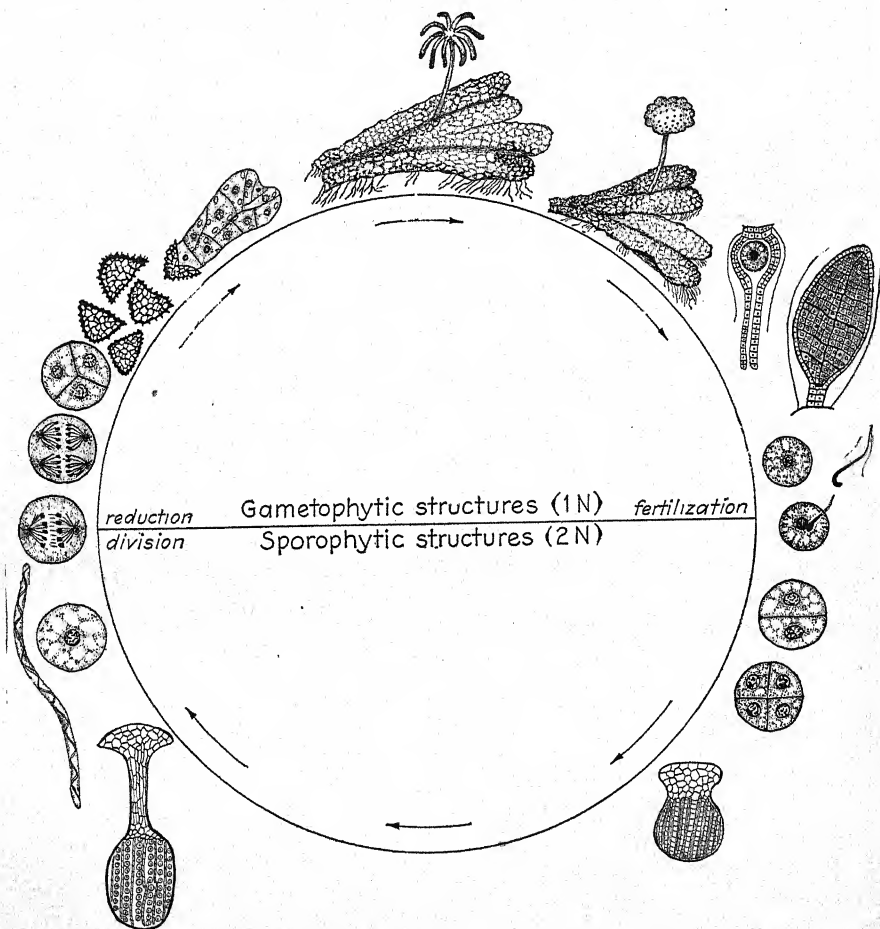


FIG. 211. Diagrammatic representation of the life cycle of the bryophyte *Marchantia*.

the calyptra, the sporophyte may be slightly green, but at full maturity it is yellowish in color and dependent upon the old gametophytic thallus for its nutrition.

The capsule is an ovoid structure at the distal end of the sporophyte. It has a wall consisting of a single layer of cells, surrounding the spore-bearing tissues, and is the most highly differentiated portion of the sporo-

phyte. Within the spore-bearing region or **archesporium** are produced isodiametric cells that will produce spores and for this reason are called **spore mother cells**, or **sporocytes**. Besides these there are slightly elongated cells which are the young elaters. The elaters develop by further elongation and the secondary deposition of material on their walls. At maturity they appear as long, narrow cells with spirally thickened walls. The twisting of the hygroscopic elaters may assist in the dispersal of spores produced in the spore case.

Meiosis and Spore Formation. As the capsule, or spore case, develops, the sporocytes, or meiocytes, increase in size, separate slightly, and become spherical in form. At the first meiotic division in each **meiocyte**, two **secondary meiocytes** are formed. A second meiotic division in each of these forms a quartet of **meiospores**. During the process the diploid number of 16 chromosomes in each meiocyte nucleus is reduced to 8 in the nuclei of each meiospore. The meiospores are thus 1N and are regarded as the first cells of the gametophytic phase. At maturity, when the capsule dehiscence in an irregular manner, the spores and elaters are released.

Development of the New Gametophyte. When the spores are released from the capsule, they fall to the ground, where, if conditions are favorable, they may germinate. Upon germination the spore produces a short filament or young thallus of several cells. Growth takes place by division of an apical cell located in the tip of the filament. As growth proceeds, the thallus develops and eventually forms sex organs and gametes (Fig. 211).

Riccia (Family Ricciaceae). The species of *Riccia* are small thallus plants growing in aquatic habitats, such as quiet, shallow ponds, swamps, and bogs. A part of their lives is spent floating on the surface of the water, and often a part on the mud at the bottom of the pond after the water has dried up during the summer months. Structurally, the thallus of *Riccia* is adapted to existence in a moist situation where the mineral nutrients are derived from the aqueous medium in which it grows. Doubtless, to a considerable extent, the carbon dioxide is derived from the water rather than from the air, much as in the case of the algae. This is especially true in *Riccia fluitans*, since much of the thallus is submerged in water.

The mature *Riccia* thallus is a small, green, dichotomously branched mass of tissue. In one species the thallus is very thin and of simple structure, almost alga-like. It attains a length of possibly 2 or 3 in. and has the form of a long, narrow, branched ribbon. The thallus of another species is heart-shaped, thicker, and more compact, the larger specimens attaining a maximum diameter of possibly $\frac{3}{4}$ to 1 in. (Fig. 212). A conspicuous midrib is a feature of the thallus, and there is considerable differentiation of tissue. The upper surface is covered by a single layer of epidermal cells. The lower surface bears rhizoids and thin scales, the latter composed mostly of a single layer of cells. Resembling the root hairs of higher plants, the rhizoids are single-celled filaments, the principal function of which is the attachment of the thallus to the substratum. Within the thallus proper there is a differentiation of tissues also. The cells of the midrib are elongated and usually lack chlorophyll. The lower portion of the thallus consists for the most part of cells with little chlorophyll. The upper

portion of the thallus is composed of chlorophyllose cells arranged in vertical rows or columns, with broad chambers of air spaces between them. No well-developed pores for gaseous exchange are found in *Riccia*. The thalli in some species have rudimentary pores, but in others, owing to the peculiarities of development of the epidermal cells, pores are entirely lacking.

The thallus of *Riccia* develops from a meiospore, as described in the discussion of *Marchantia*. *Riccia* is without specialized methods of asexual reproduction but may be vegetatively multiplied by fragmentation. As growth progresses and the older portions of the thallus decay or are broken, the younger branches may be separated and grow into new plants.

The Life Cycle. The essential features of sexual reproduction of *Riccia* are the same as those in *Marchantia*. Structurally the antheridia and archegonia are alike in both genera. Their positions on the thallus, however, are different. The sex organs

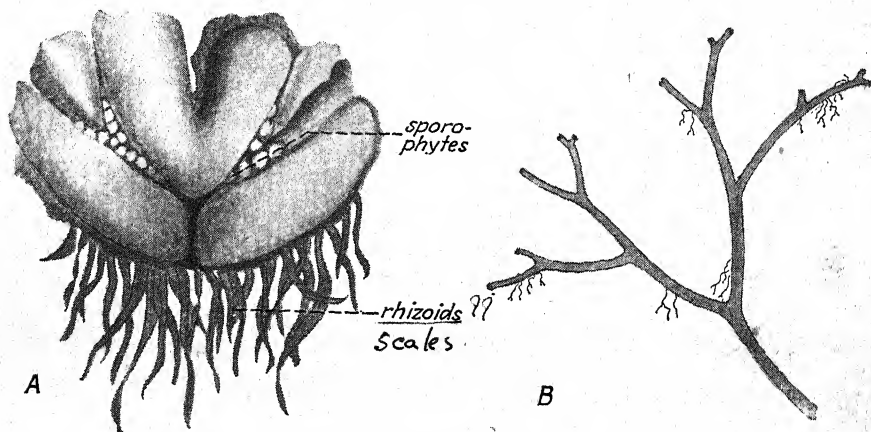


FIG. 212. Vegetative features of some lower liverworts: A, *Riccia natans*, gametophytic thallus with sporophytes and rhizoids; B, *Riccia fluitans*, showing rhizoids. (Drawings by Elsie M. McDougle.)

of *Riccia* develop from segments of the apical cell located in the tip of the thallus. The antheridia are usually developed first in a young thallus. Development of archegonia follows later in the same thallus. As the thallus grows, new vegetative tissue forms at its apex, building the thallus up in advance of the young sex organs. As growth progresses, the sex organs appear distributed along the midrib, with the antheridia toward the base and the archegonia nearer the apex of the thallus. At maturity, the gametangia are found deeply sunken in the thallus, each one in a separate cavity near the midrib (Figs. 212, 213).

The sporophyte develops from the zygote and at maturity is a spherical body consisting of a central mass of spores surrounded by a wall one layer of cells in thickness. The entire sporophyte, completely dependent upon the gametophyte, is enclosed in the enlarged venter of the old archegonium, now called the calyptra. The combined structures, sporophyte, and calyptra are embedded in the thallus (Fig. 213, C).

Spores are released from the sporophyte by decay of the thallus tissue and the wall of the sporophyte. Upon germination they grow, producing new gametophytes.

Summary of the Marchantiales. The complete life history of a liverwort consists of two distinct alternating phases, the gametophytic and the sporophytic. These phases differ in their manner of origin, their chromosome numbers, their structure, and in the degree of their physiological independence. They are both essential, equally important, and the two make a unit life cycle.

During the gametophytic phase, all structures of the gamete-bearing plant, or gametophyte, have the haploid number of chromosomes. The structures formed during the gametophytic phase are the meiospore, which is developed following meiosis, and the thallus with all its parts, which grows from the germinating meiospore. As the thallus reaches maturity,

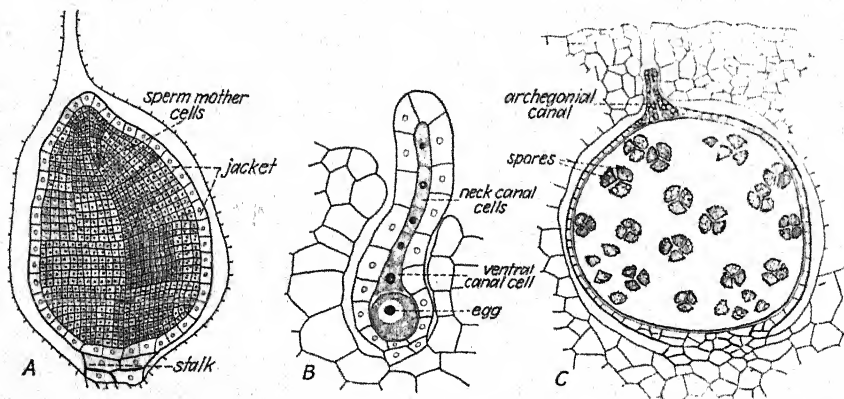


FIG. 213. Reproductive structures in *Riccia*. A, mature antheridium; B, mature archegonium; C, mature sporophyte embedded in gametophytic tissues.

the sex organs or gametangia are formed. Gametes produced in the sex organs, sperms in the antheridia, and eggs in the archegonia are the last structures developed by the gametophyte.

Union of the gametes during fertilization initiates the sporophytic phase with the zygote its first cell. The embryonic, or young, stages of the sporophyte are developed through growth and division of the zygote. Sporophytes of the Marchantiales vary in form and complexity, but they are all relatively simple structures. As they grow, sporogenous tissue is formed in the capsule of the sporophyte. Finally, numerous sporocytes develop. *Meiosis with a reduction of chromosomes from the diploid to the haploid number occurs in each sporocyte.* As a result of two meiotic divisions, a quartet of meiospores is formed from each sporocyte. *This initiates a new gametophytic phase with the meiospore as its first cell.* A regular alternation of chromosomes from the haploid to the diploid numbers ac-

companies the alternation of structures during the gametophytic and sporophytic phases. The *periodic occurrence of syngamy and meiosis* in the life cycle *keeps the haploid and diploid chromosome numbers in equilibrium* during the alternating phases.

ORDER II. JUNGERMANNIALES—LEAFY LIVERWORTS

The members of the order Jungermanniales may be found growing on damp soil and rocks or on decaying logs. Some forms are epiphytic on tree trunks in damp forests. Decaying logs along the banks of streams are frequently completely covered with the

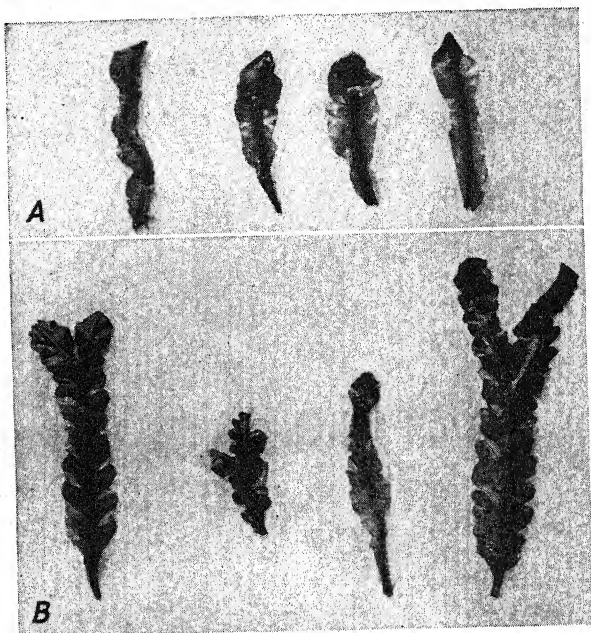


FIG. 214. Vegetative structures of thallose Jungermanniales. A, *Pallavicinia*; B, *Symphyogyna*.

leafy forms, recognizable by their unusually elaborate and delicate thalli, resembling lacework.

The Jungermanniales are subdivided into two groups, the **Anacrogynae** and the **Acrogynae**. The Anacrogynae are characterized by the development of the archegonia on the dorsal surface of the thallus, never at the apex. Correlated with this position of the archegonia is the thallose type of plant body which is not characteristic of the order as a whole (Fig. 214). The Acrogynae are characterized by the development of the archegonia at the apex of the thallus. Correlated with this location of the archegonia is the foliose type of plant body. In this group the thallus is deeply lobed, forming leaf-like structures on a central axis, and it is from this group that the common name of the order "leafy liverworts" is derived (Fig. 215, A).

With reference to other liverworts, the position of the Jungermanniales can best be represented by considering them as a group of plants paralleling the members of the Marchantiales but emphasizing different tendencies in the evolution and develop-

ment of the gametophyte and showing a more highly developed sporophyte. The gametophyte is characteristically elaborate in form. The elaborate leafy form is correlated with a simple internal structure and but slight tissue differentiation. These two features are in sharp contrast to the situation in most members of the Marchantiales, which have thalli very simple in form but with considerable complexity of structure and tissue differentiation.

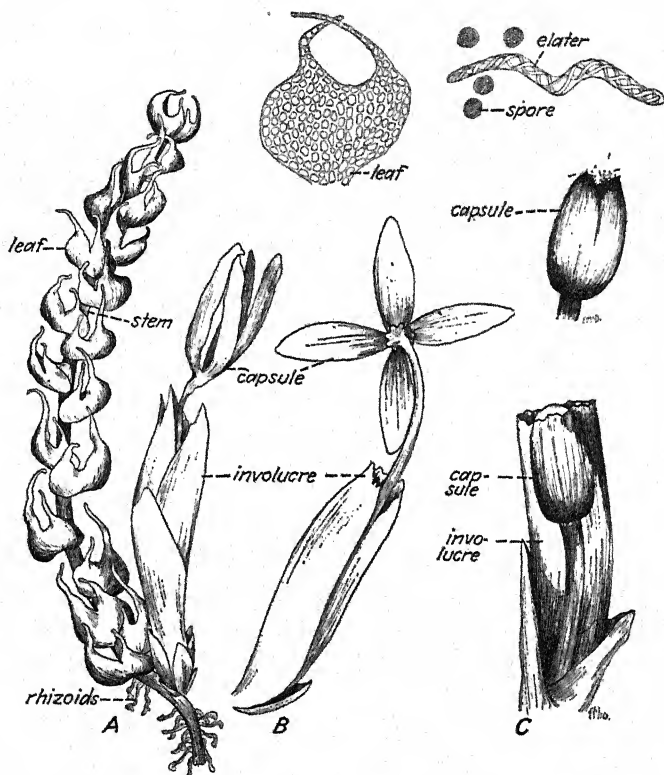


FIG. 215. Structural features of *Cephalozia*, a member of the foliose Jungermanniales. A, plant showing so-called leaves, enlarged above, stem, rhizoids, and capsule arising above involucre, on a branch; B, capsule showing appearance after dehiscence; C, detail of capsule, the upper figure indicating spore dispersal.

The thalli of the Jungermanniales show the evolution and development of a diversity of form ranging from a slender ribbon-like thallus similar to that of *Riccia fluitans* and the smaller genera of the Marchantiaceae to delicate, elaborately lobed structures presenting the appearance of leaves attached to a central axis (Figs. 214, 215). Almost all gradations in indentation of margins occur. In fact, an evolutionary series in the development of form in these genera can be arranged. The leafy thalli sometimes resemble the plant bodies of some of the creeping mosses. Close examination, however, reveals that the leaf-like structures of liverworts are attached to two opposite sides of the stem and that the thallus is really dorsiventral in symmetry.

In the mosses, on the other hand, the leaf-like organs are arranged around the stem with the symmetry radial rather than dorsiventral.

The mature antheridia and archegonia in general resemble those of the members of the Marchantiales, differing only in certain minor respects. The antheridia are usually spherical structures borne on comparatively long stalks. The archegonia are typical flask-shaped structures but usually more massive than the corresponding structures of Marchantiales (Fig. 216, A, B). The details of development of the antheridia of the Jungermanniales differ from those of the Marchantiales, but the development of the archegonium in the two orders is quite similar.

The sporophyte structure of the Jungermanniales is, in general, very much more elaborate than that of the Marchantiales. At maturity it consists of the foot, the long flexuous stalk, and an oval capsule (Figs. 215, B, C; 216, H).

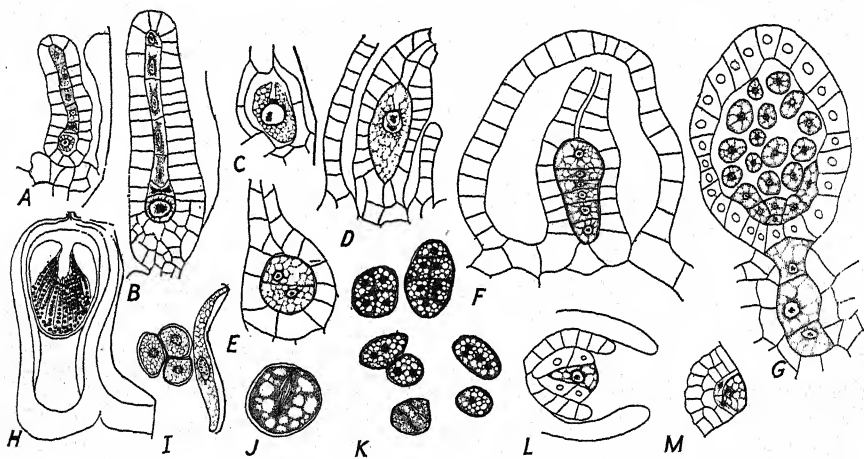


FIG. 216. Some structural details of members of the Jungermanniales. A, archegonium of *Pellia*; B, archegonium of *Porella*; C and D, fertilization stages and, E, first embryonic division in *Sphaerocarpus*; F, young sporophyte and, G, older sporophyte of *Sphaerocarpus*; H, diagrammatic representation of elaterophore of sporophyte of *Aneura*; I, spore mother cells and elater from *Aneura*; J and K, spores of *Pellia* germinating; L, apical cell of *Porella* and, M, of *Pellia*.

The structure and manner of dehiscence of the capsule of the sporophyte are characteristic of most genera of the order. The elaters are attached to a structure called the elaterophore, which is a mass of sterile tissue of varying size located in the tip of the capsule (Fig. 216, H). The capsule wall naturally and regularly opens along four longitudinal lines of dehiscence and at maturity breaks into four valves (Fig. 215). This regular method of dehiscence is also a feature in contrast to the capsule of the Marchantiales which opens irregularly.

ORDER III. ANTHOCEROTALES—HORNED LIVERWORTS

a/ The order Anthocerotales represents a very small group of liverworts consisting of three genera, viz., *Anthoceros*, *Megaceros*, and *Notothylas*. The latter two are tropical. *Anthoceros*, the only genus found in temperate regions, usually occurs on very moist clay banks, frequently along hillside roads where the clay is "seepy." There is some question as to the position of the order taxonomically, but it is con-

veniently and commonly regarded as an order coordinate with the Marchantiales and the Jungermanniales.

The noteworthy features of the members of the Anthocerotales are the very simple form and structure of the thallus, the sunken sex organs, and, most prominent of all, the high development of sporophyte structures (Figs. 217, 219).

The thallus, in comparison with that of other liverworts, is simple in structure. It is as simple in form as that of the most primitive forms of the Marchantiales. It lacks differentiation in external form and internal structure. Simplicity is its prominent feature.

An unusual feature of the cells of the gametophyte is the presence of a single chloroplast which contains a pyrenoid. Pyrenoids are characteristically present in the chloroplasts of the cells of algae but are unknown elsewhere, with the exception of the *Anthoceros* thallus (Fig. 218, *H*).

Both archegonia and antheridia are developed within the tissues of the thallus, rather than superficially as in other liverworts. It will be remembered that, although the sex organs may appear sunken in other forms, they actually develop superficially and come to lie in pockets formed by the more rapid growth of thallus tissue immediately surrounding the sex organs. In *Anthoceros*, the antheridia are borne in groups sunken in the thallus. The archegonia are not so completely embedded as the antheridia, but the wall of the venter and part of the neck are confluent with the tissues of the thallus (Fig. 218).

The structure of the sporophyte is the feature of greatest interest in the order (Fig. 219). It is a slender cylindrical structure of fairly uniform thickness throughout its length, consisting of a foot and capsule. It stands erect upon the thallus to which it is attached by means of the foot. The structure of the capsule is complex. There is a central region composed of sterile cells called the columella. In transverse section the columella shows 16 cells in rectangular arrangement. Surrounding the columella is a cylinder of sporogenous tissue, which in turn is surrounded by a cylinder of sterile tissue and finally the epidermis. In the cylinder of sporogenous tissue, alternating layers or bands of sterile and spore-producing cells occur. In the spore-producing bands, sporocytes, or spore mother cells, eventually round off, undergo meiosis, and give rise to spores. The outer tissues of the capsule are abundantly supplied with chlorophyll, which enables them to synthesize carbohydrates. The ability of the sporophyte to carry on photosynthesis is more highly developed in this group than in any other of the liverworts. Stomata are present in the epidermis of the sporophyte.

A feature not shown at all by the sporophytes of any other liverworts is the presence in the *Anthoceros* capsule of a mass of meristematic tissue located in the lower portion of the capsule, which provides for continued growth of the capsule over an extended period and prolongs the period of spore production. Mature spores may be found in the tip of the capsule while the meristematic tissue at the base is still giving rise to

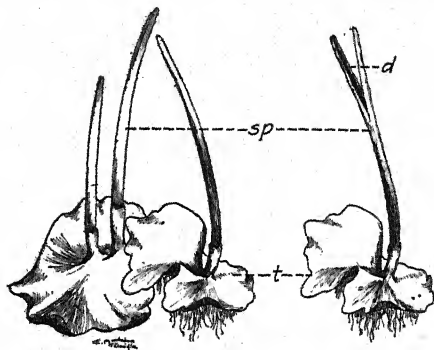


FIG. 217. Habit of *Anthoceros*, thalli, *t*, sporophyte, *sp*, showing dehiscence, *d*. (Drawings by Elsie M. McDougle.)

sporocytes. At maturity, the capsule dehiscs into two valves and its appearance at this time justifies the common name "horned liverworts" often applied to them.

The *Anthoceros* sporophyte, with its alternating layers of sterile and spore-producing tissue, is highly specialized. Bower, a British botanist, has made the arrangement of sterile and spore-producing tissue in the capsule of the Anthocerotales the basis of a theory for the origin and evolution of leaves and sporangia of the higher plants.

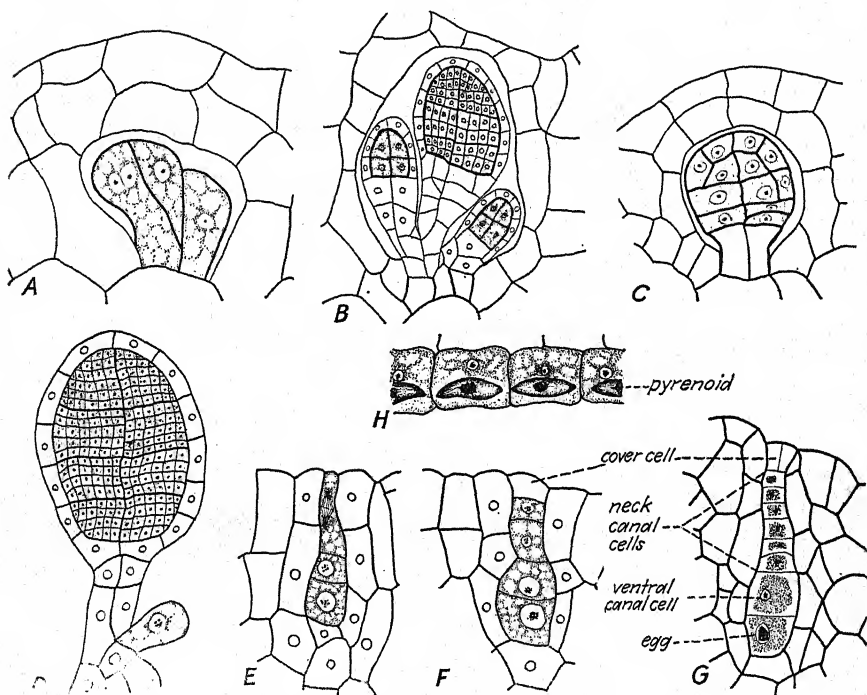


FIG. 218. Some structural details of *Anthoceros*. A-D, stages in development of antheridia; A and B show development by budding of several antheridia in a chamber; D, mature antheridium; E-G, stages in development of archegonium; E shows spindle in cell dividing to form cover cell and primary neck canal cell; G, mature archegonium; H, detail of vegetative cells from thallus with the characteristic pyrenoids.

THE MUSCI—MOSSES

GENERAL FEATURES

The mosses, a large group of plants, constitute the higher bryophytes. They are world-wide in distribution, growing in every kind of habitat from aquatic to xerophytic. The majority of the species of mosses, however, grow in moist situations, such as moist woodlands. Because of their ability to grow in drier and, therefore, more generally frequented situations, the mosses are much better known to the average person than are the liverworts.

The conspicuous part of the moss plant consists of the more or less erect stem which bears expanded leaf-like structures. Root-like strands, known as rhizoids, anchor it to the substratum. The leafy stems are scientifically known as the **gametophores** because they bear the sex organs and the

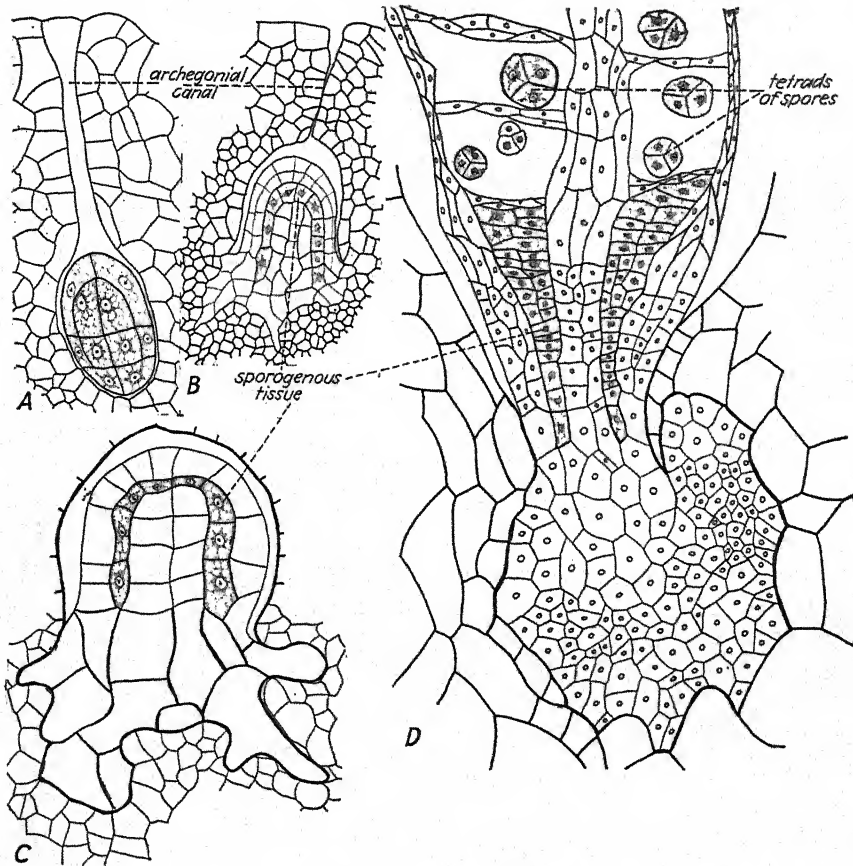


FIG. 219. Development of the sporophyte in the Anthocerotales. A-C, *Anthoceros*; A and B show old archegonium canal; B and C show sporogenous tissue; D, somewhat diagrammatic drawing of sporophyte of *Notothylas* with tetrads in sporogenous region.

gametes. After fertilization, the sporophyte is developed at the apex or on the side of the gametophore.

The outstanding structural features which distinguish mosses from liverworts are the alga-like **protonema** which develops from the spore, the radial symmetry of the leafy stems, and the elaborate capsule produced on the mature sporophyte. The mosses are divided into three orders, the **Sphaginales**, the **Andreaeales**, and the **Bryales**. The first and

the last of these are the best known and are considered in some detail in the following pages.

THE ORDER SPHAGNALES

General Features. The order Sphaginales contains the single genus *Sphagnum*, the bog or peat moss, which is represented by several hundred species of world-wide distribution. These mosses grow only in moist situations. Their favorite habitat is an old pond or lake where, in many cases, growth of the *Sphagnum* is the primary cause of the filling up of such bodies of water. *Sphagnum* bogs are very interesting

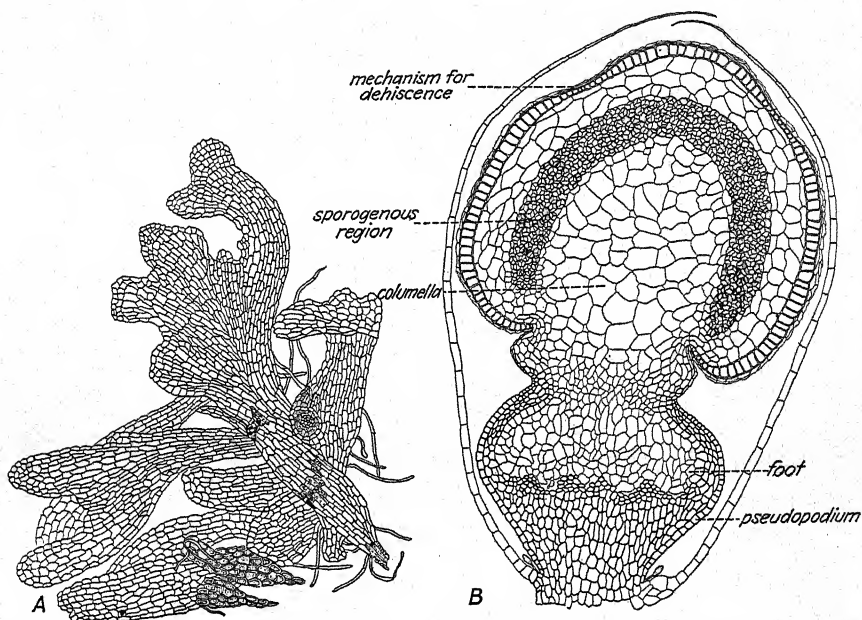


FIG. 220. A, young, thallose gametophyte of *Sphagnum* with rhizoids and bud from which the erect gametophore may arise; B, sporophyte. (Drawings by Laura K. Wilde.)

ecologically since the elimination of many of the more usual types of plants by the acidity and other unfavorable characteristics of the bog results in the development of unusual plant associations.

Sphagnum is of considerable commercial importance. Peat, used for fuel in some regions, is composed of carbonized *Sphagnum* and its bog-plant associates. *Sphagnum* is gathered and dried and, upon remoistening, is extensively used for packing living plants for shipment. Certain species of the genus, on account of their superior absorptive powers, are used for surgical dressings in hospitals.

The structural features of *Sphagnum*, some of which resemble the liverworts, and others the higher or true mosses, indicate that *Sphagnum* occupies an evolutionary position somewhere between these two groups of bryophytes.

The Gametophytic Structures. Upon germination, the spore produces a very short filament which eventually forms a branched thallus body resembling that formed by some of the liverworts (Fig. 220, A). By budding, the thallus body forms erect

branching structures which, upon maturity, become the gametophores and are the recognized "Sphagnum plants" (Fig. 221). These resemble the similar structures of the true mosses (Bryales). The gametophores consist of a central stem-like axis with numerous branches which are covered with leaf-like expansions. The branches of the gametophores are of two kinds, short erect branches, which, clustered near the apex, form a sort of rosette, and long pendant structures, which fall gracefully around the stem (Fig. 221). The short erect branches produce the sex organs. *Sphagnum* plants are either monoecious or dioecious; but even when both kinds of sex organs are on the same gametophore, the antheridia and archegonia are produced on separate branches.



FIG. 221. Plant of *Sphagnum* with both gametophyte, *g*, and sporophyte, *sp*.

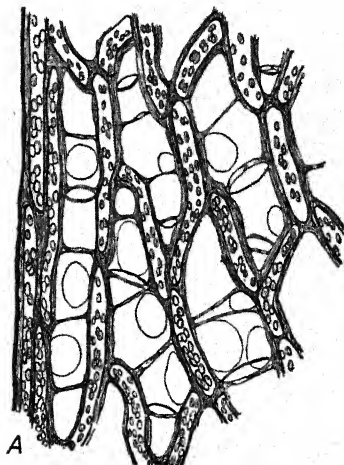


FIG. 222. Structural features of *Sphagnum*. *A*, surface view and *B*, transverse view of cell structure in leaflike organs. (Drawing by John Shuman.)

The stem, branches, and leaves of the gametophore have a relatively complex structure which varies with the different species (Fig. 223, *I, J*). The stems and branches consist of a central mass of tissue and an outer region. The cells of these two regions are differentiated, those of the central portion being elongated in the vertical direction. The leaf-like structures are made up of two kinds of cells, large hyaline cells, often with conspicuous thickenings and large pores, and continuous chains of small elongated cells which contain the chloroplasts (Fig. 222). When a portion of the leaf is magnified, the small cells appear in a reticulate formation in the leaf structure with the large hyaline cells occupying the "meshes" of the network. The absorptive properties of *Sphagnum* are probably to be attributed to the water-holding power of the hyaline cells of the "leaves".

The antheridia at maturity are spherical bodies borne on long stalks and located

on the short erect branches in the axils of the so-called leaves (Fig. 223, A-G). The sperms are elongated, spirally curved structures and are biciliate. The archegonia, which in general resemble those of *Marchantia*, are produced on the ends of the erect branches; at maturity they are relatively large structures with stalk, long neck, and massive venter. The egg cell is relatively small and of about the same size as the ventral canal cell, which it greatly resembles (Fig. 223, H).

The Sporophytic Structures. The sporophytes of *Sphagnum* are generally regarded as of rare occurrence. Their scarcity probably results from the infrequency of fertilization, which in turn appears to be correlated with the water level in the bogs where *Sphagnum* grows. When found, the sporophytes are generally located on

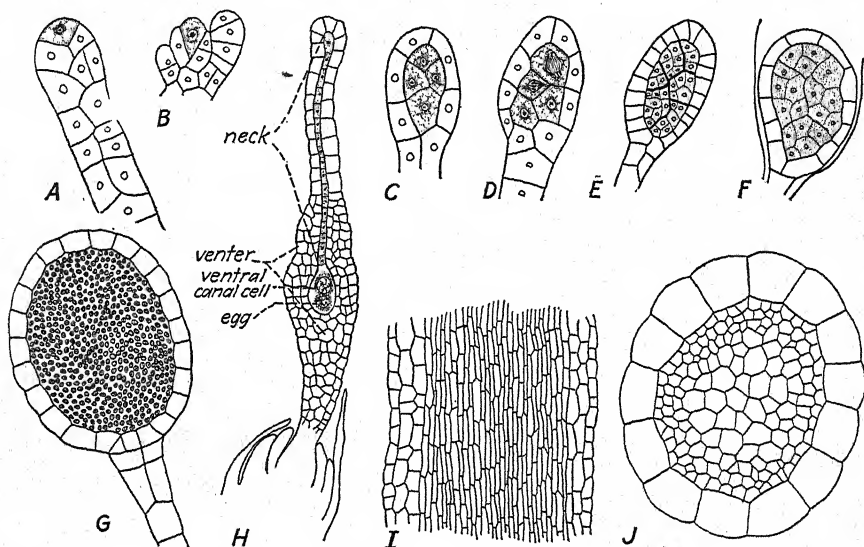


FIG. 223. Some structural features of *Sphagnum*. A and B, apical cells; C-F, stages in development of young antheridia; G, mature antheridium; H, mature archegonium; I, longitudinal, and, J, transverse, section of stem, showing slight differentiation in tissue. (G, I, and J drawn by Helen D. Hill.)

plants growing in clumps upon little knolls or hummocks in the bog or perhaps in depressions. The water level may be either too high or too low for the sperms to reach the archegonia. Investigators have secured abundant sporophytes by artificially applying the sperms to the female plants at the time when the eggs are mature within the archegonia.

The zygote, formed by the union of the sperm with the egg, develops into the sporophyte, which eventually produces the spores by the maturation processes. The mature sporophyte is small, consisting of a spherical capsule, dark brown or black in color, a very short seta or stalk, and an expanded foot, which serves to attach the sporophytic structures to those of the gametophyte (Figs. 220, B, 221). The growth of the pseudopodium, or false foot, a gametophytic structure, elevates the sporophyte above the apex of the branch which bore the archegonium containing the egg. The pseudopodium is an outgrowth of the apex of the branch and is a portion of the haploid, or gametophytic, structures. The dome-shaped spore layer, or archesporium, formed

within the capsule resembles the spore layer in the capsule of the liverwort *Anthoceros* (Fig. 220, B).

THE ORDER BRYALES—THE TRUE MOSSES

The mosses comprise a group of small, green, mostly terrestrial plants of wide distribution. Some of them grow in exposed and rather dry situations as on the surface of rocks and on tree trunks. Most of them, however, are found in moist and, frequently, in shaded locations. A few grow submerged in water. Multicellular rhizoids attach the plant to the substratum. Moss plants vary in size from specimens scarcely visible without the aid of a hand lens to large forms, like the water moss *Fontinalis*, often a foot in length. In general they are more slender and delicate than the thallose liverworts, but at the same time they are more complex. Some grow as single erect structures, and others are branched. The branched types may have a prostrate stem growing horizontally on the surface of the substratum from which arise erect branches. Moss plants are elaborate in form, resembling the leafy liverworts in this respect. The main axis of a moss plant is usually called a "stem," and its expanded parts "leaves." These structures belong to the $1N$, or gametophytic, phase of the life cycle and are not homologous with the true stems and leaves of the flowering plants, which are $2N$ and are borne on the sporophyte. The stems and leaves of the flowering plants have attained a higher structural development and they have greater differentiation of tissues than the analogous parts of the mosses. True leaves and stems have a well-differentiated epidermis with stomata and guard cells. There is a vascular system serving as conducting tissue and for support in the leaves and stems of all higher plants. The stems and leaves of mosses lack these well-developed structures.

The stems of mosses are differentiated into an epidermal layer, a cortical region of mostly isodiametric, thin-walled cells, and a central core composed of thick-walled cells that are of small diameter and somewhat elongated. The epidermis of moss stems lacks stomata. Epidermal cells and those in the younger cortex are generally chlorophyllose. It is thought that the central core functions as supporting rather than conducting tissue. Stems of the moss plants, which may be either branched or unbranched, increase in size through the activity of a single apical cell which rarely may have two but more frequently three cutting faces. Similar apical cells are also present in the growing points of branches. In their young stages, the position of the leaves is determined by the type of apical cell in the stem apex. An apical cell with two cutting faces determines that the leaves will occur in two ranks. The three-faced apical cell gives rise to a radial arrangement of leaves, which occur in three ranks. As the plant develops, the leaves tend to lose their definite positions and may no

longer appear in vertical rows. All three ranked types, however, maintain their radial arrangement. The structure and complexity of moss leaves vary in the different kinds of mosses. In some mosses, the leaves have only one layer of similar cells making up the blade. Usually there is a midrib of several layers of cells. Mosses with delicate leaves of simple structure usually grow in moist, shaded locations. Other mosses, often growing in dry localities, have leaves composed of many cell layers with differentiation of tissues.

The Gametophytic Phase. The adult moss plant, the most conspicuous part of the life cycle, normally is a $1N$ structure. These plants are game-

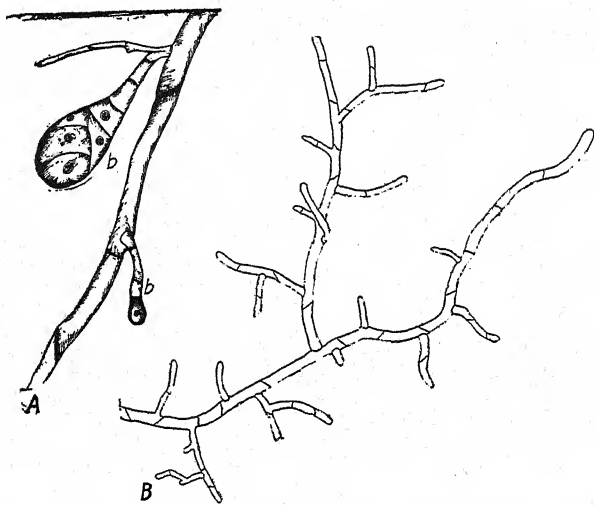


FIG. 224. Moss protonema, A, with bulbils, *b*; B, general habit of growth.

tophytic structures, but they do not represent the entire gametophyte. Structures produced during the gametophytic phase include (1) the *meiospores*; (2) the *protonema* which grows from a germinating meiospore; (3) the erect *gametophores* which grow from buds on the protonema; (4) the *sex organs*, or gametangia, antheridia, and archegonia; (5) their *gametes*, sperms and eggs, which are produced on the moss plants. The **protonema**, or first thread, is an inconspicuous filamentous alga-like structure. The protonema develops into two forms; one growing prostrate upon the surface of the substratum or sometimes slightly aerial is composed of short cylindrical cells, each with nucleus, chloroplasts, and cytoplasm. The second form penetrates the substratum. In this, the cells tend to lose their chlorophyll, and the cell walls become brownish in color. As the protonema grows older, the cross walls assume an oblique

position, and the whole structure becomes rhizoidal (Fig. 224, B). The leafy moss plants develop from buds formed on the protonema. The plants may therefore be regarded as erect, highly developed branches of the protonema. Several buds may develop on a single protonema. This

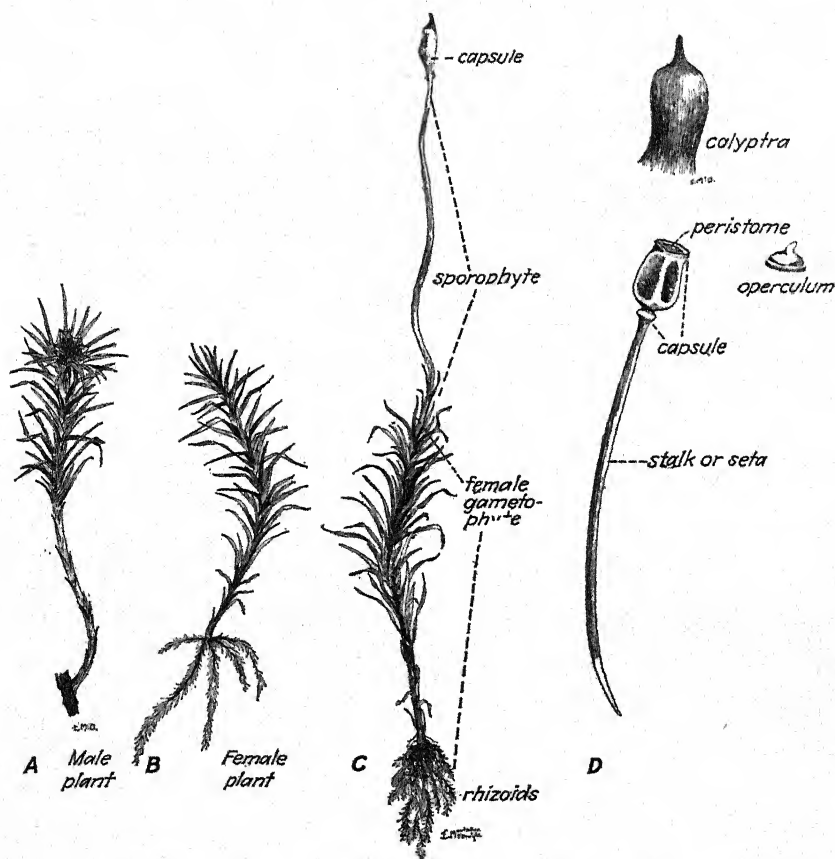


FIG. 225. *Polytrichum commune*, a common moss. A, male gametophyte; B, female gametophyte; C, female gametophyte with sporophyte; D, sporophyte parts enlarged.

accounts in part for the occurrence of moss plants in clumps. After the erect leafy plants are established, the protonemal structures may disappear or persist. Septate rhizoids, which resemble the protonema, grow from the bases of the moss plants. The rhizoids serve to attach the plant to the soil and to absorb moisture and minerals from the soil. The sex organs, or gametangia, develop at the apex of the plant or at the ends of

branches. This feature and the fact that they arise from the prostrate protonema suggests that the erect leafy moss plants are in reality gametophores, homologous with the erect gametophores growing on the thalli of *Marchantia*.

The Sex Organs. The sex organs, or gametangia (Figs. 226, 227), are produced terminally, either on the main axis of the gametophore or on its side branches. Some species are hermaphroditic, with both kinds of gametangia borne on the same plant, either together or slightly separated.

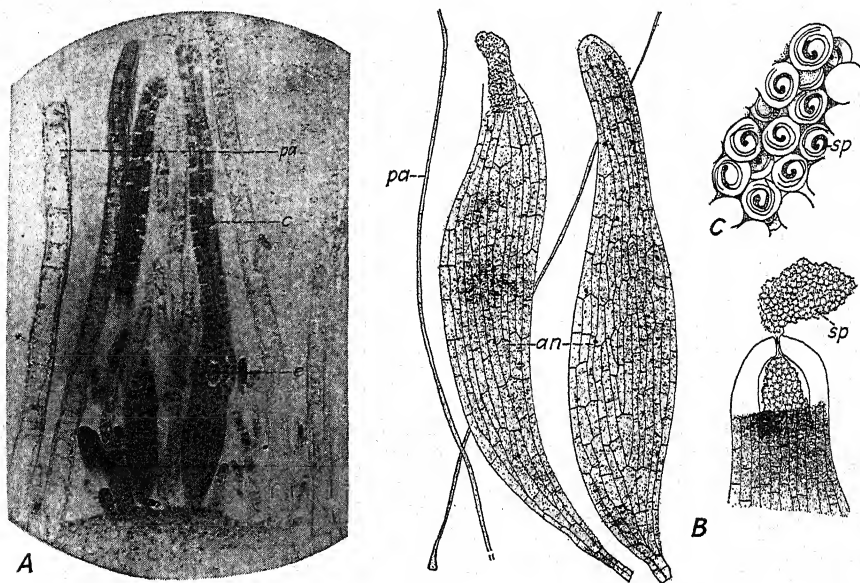


FIG. 226. Sex organs of common moss. *A*, showing archegonium with egg, *e*, and long canal, *c*, paraphyses, *pa*; *B*, two antheridia, *an*, at left and paraphyses, *pa*; tip of antheridium enlarged, at right, to show sperms, *sp*, emerging; *C*, biciliate sperms, *sp*, enlarged.

Other species are dioecious with the male, or microgametangia, and female, or megagametangia, borne on separate plants. These may be called male, or antheridial, plants and female, or archegonial, plants. In some species male and female plants may be strikingly different and may be recognized at a glance (Fig. 225).

The mechanism of dehiscence of the antheridium generally consists of one or two large cells that form a cap at its apex. When a mature antheridium is wet, the wall cells absorb moisture and swell. Pressure within the wall cells, including the larger cap cells, may become sufficient to burst the cap cells or to break their connections with adjacent cells, thus freeing the mass of sperms.

Fertilization. Fertilization, or syngamy, in the mosses occurs when a haploid sperm, or microgamete, fuses with the haploid egg, or megagamete, and forms the diploid zygote. Since this union marks the beginning of the diploid or sporophytic phase, it is one of the two critical points in the reproductive cycle. A stimulus to growth following fertilization is expressed in the development of the embryo, or young stage, of the sporophyte (Fig. 228).

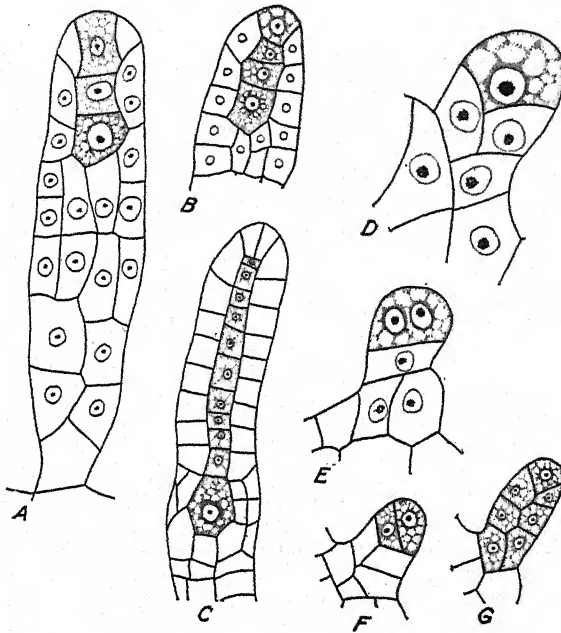


FIG. 227. Stages in development of sex organs of moss. A and B, young archegonia; C, mature archegonium; D–G, early stages in the development of antheridia.

The Sporophytic Phase. The zygote formed at fertilization is the first cell of the diploid or sporophytic structure. The first division of the zygote is transverse to the long axis of the archegonium. This is followed by other divisions which finally form apical cells in both the upper and lower ends of the elongating embryo (Fig. 228). The early development of the sporophyte is largely a sequence of cell divisions and growth of the resulting cells. Since the zygote is located in the archegonium, all the early stages of embryonic development take place within the venter of the archegonium. As the embryo increases in size, the tissues of the archegonium are also stimulated to growth and there is a corresponding enlargement of the venter.

The Mature Sporophyte. Later development of the embryo results in the production of the mature sporophyte with its elaborate structural and cellular differentiation. The mature sporophyte consists of (1) a **foot** embedded in and attaching the sporophyte to the apex of the old gametophore, (2) an elongated **stalk**, or **seta**, connecting the foot, and (3) the **capsule**, or spore case, surmounting the structure. Only slight tissue differentiation is shown by the foot, which is embedded in the apex of the gametophore. Water and minerals in solution, necessary for the life and

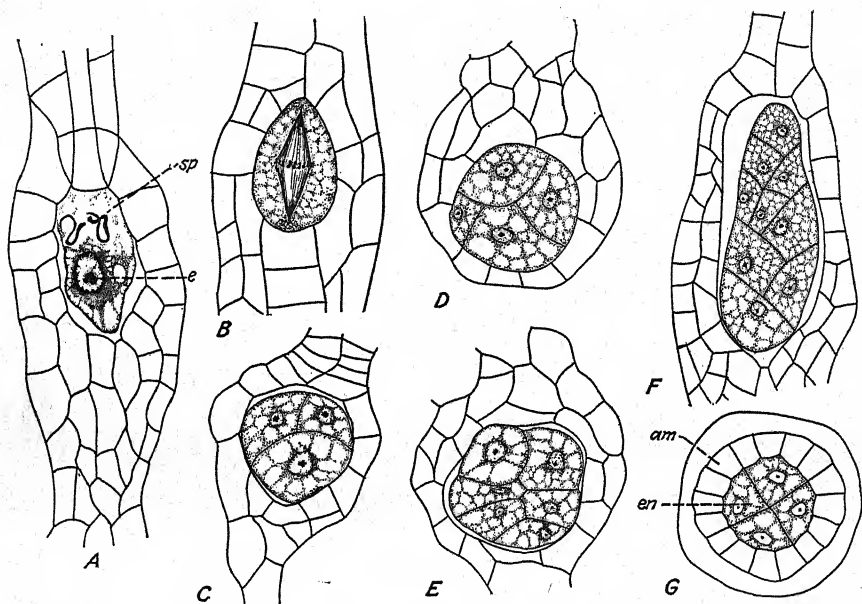


FIG. 228. Development of sporophyte of a moss. A, early stage of fertilization; egg, *e*, and sperms, *sp*; B-F, a series of stages in growth of the sporophyte; G, transverse section of a young capsule showing amphithecium, *am*, and endothecium, *en*.

growth of the sporophyte, are absorbed from the gametophytic tissues. The stalk, or seta, shows more differentiation than the foot. A well-defined central strand of small thin-walled cells may conduct water but is not a true vascular strand. A layer of thick-walled cells that may serve as supporting tissue surrounds the central strand.

The distal end of the sporophyte is differentiated into an elaborate spore case or capsule. Moss capsules are of various shapes; they may be almost spherical, pear-shaped, or flattened. Some of them are of an elongated ovoidal form, and many are shortened cylindrical structures. Most moss capsules are circular in cross section. Their position may be erect, partly

or completely inverted, and pendant at the apex of the stalk. Structurally, the capsule consists of an upper urn-shaped portion, the **theca**, where the spores are produced, and often an enlarged, sterile portion at the base, the **apophysis**. An apical covering in the form of a cap is called the **operculum**. This structure, a part of the mechanism of dehiscence, takes its name from a kind of cap worn by some of the Roman soldiers. At the base of the operculum is a ring of cells forming a structure called the **annulus** made up of two kinds of cells. Those in the upper portion are modified by heavy thickenings on the walls, while those below and at the junction of the operculum and the theca are thin-walled cells. The cells around the upper part of the theca are also thickened. A region of thin-walled cells between these two rings of heavy ones forms a line of structural weakness between the operculum and the main body of the capsule. As the capsule matures, the thin-walled cells dry out and break and, in this way, the operculum is released; eventually it is shed, thus opening the capsule.

Beneath the cap, or operculum, there is a ring of pointed multicellular structures called **teeth**. Collectively the teeth constitute the **peristome**, so named because of its position surrounding the mouth of the capsule. The peristome is made up of one or more rows of teeth of varying number. The number and structure of the teeth are used as characters in the determination of the genera and species of the mosses. During periods of dampness, the teeth curl inward tending to close the mouth of the capsule. When they are exposed to dry conditions, the teeth curl outward opening the capsule. Because of the hygroscopic nature of the teeth, spores are likely to be shed in dry weather when conditions for dissemination are favorable.

In the mosses, generally, there is an additional covering called the **calyptra**, carried over the apex of the capsule and external to the operculum. The calyptra is not actually a part of the sporophyte but is a structure developed through the enlargement of the old archegonium. As the zygote in the venter of the archegonium starts growth, the tissues of the archegonium also grow. During the early stages of development, the growth of the calyptra parallels that of the sporophyte, and for a time the sporophyte and the archegonium enlarge proportionally. Eventually, however, the sporophytic tissues outgrow those of the archegonium. The tension is relieved by the rupture of the archegonium at its base. Thus freed, the old archegonium, now called the calyptra, is carried as an apical covering of the sporophytic capsule (Fig. 225). Although the entire sporophyte is diploid tissue, the calyptra originating as the archegonium is haploid tissue.

Differentiation of Tissues in the Capsule. There is considerable differentiation of tissues in the capsule. A well-defined epidermal layer

with stomata and guard cells, resembling those of the higher plants, covers the capsule. The stomata open into large intercellular cavities in the capsule, as in the higher plants. Just beneath the epidermis is a region, two or more layers of cells in thickness, that forms the wall of the capsule. The apophysis is a mass of sterile tissue often present as a bulbous enlargement in the lower portion of the capsule. Chlorophyllose tissue and stomata are abundant in this part of the capsule, although not restricted to this region. In the capsules of some mosses there are radial columns of chlorophyllose cells beginning in the apophysis and extending upward into the capsule. Within the capsule are two portions, an inner group of tissues, the **endothecium**, and an outer group, the **amphithecium**. These portions are differentiated during the development of the embryo. The endothecium consists of a central mass or core of tissue, the **columella**, and a cylindrical sporogenous layer, the **archesporium**, surrounding it. The amphithecium forms the outer layers of the capsule (Fig. 228, G).

Meiosis and the Formation of Meiospores. As the capsule develops, large numbers of sporocytes are finally formed in the sporogenous layer. Each of these sporocytes undergoes meiosis, forming a quartet of meiospores. Since the sporocytes are diploid structures, the meiotic divisions result in the reduction of the chromosomes to the haploid number in each of the meiospores. During the maturation of the spores, which are the first cells of a new gametophytic phase, they develop thick walls previous to being shed. At maturity of the capsule, very large numbers of the spores are found in a cylindrical or barrel-shaped mass surrounding the remnants of the central columella.

Vegetative or Somatic Multiplication. The mosses have several methods of multiplication. The protonemata branch extensively and form numerous buds which develop the leafy moss plants. Decay of the older parts of the protonema leads to the separation of these plants as independent entities. Small bulbils may also develop on the protonema. These become resting structures, which tide the organism over periods generally unfavorable to vegetative growth (Fig. 224, A). Small, green, multicellular buds, or gemmae, are developed on many moss plants. When these fall to the ground, they may grow into new plants. They resemble the gemmae produced on the thalli of *Marchantia*. Secondary protonemal structures may develop from almost any part of a moss plant. They develop from moss stems, the rhizoids, and other structures. It has been possible in experimental material to induce artificially the production of protonemata from the diploid or sporophytic structures. These protonemata had the diploid number of chromosomes and eventually developed diploid gametophores, bearing sex organs with diploid gametes. Fusion of these diploid, or $2N$, gametes produced $4N$ sporophytes.

Summary of the Order Bryales. The members of the order Bryales have numerous methods of vegetative multiplication and well-developed methods of sexual reproduction. The gametophytes are rather highly organized structures with numerous means of asexual reproduction. The plants live under various ecological conditions in many different kinds of habitats. The sporophytic structures are also highly developed and fairly complex. The elaborate mechanism of dehiscence of the capsule is the outstanding feature of sporophytic structures. As in the liverworts, the complete life cycle of a moss consists of two distinct phases, the haploid gametophytic and the diploid sporophytic phase, which regularly alternate during the life cycle. The first cell of the gametophyte, the meiospore, gives rise to the protonema. The gametophores, generally recognized as the moss plants, develop from the protonemata and in turn produce the gametes, sperms, and eggs in the antheridia and archegonia. The zygote formed at syngamy is the first cell of the sporophyte. From this the mature sporophyte is formed. The parts of the sporophyte are foot, stalk, and capsule.

The Phylogenetic Position of Bryophyta. Groups of plants, undoubtedly related as are the orders of the bryophytes, are difficult to place on a definite scale of development. This point is made clear if an attempt is made to list the orders and families of the bryophytes according to their degree of development. Each order has advanced in certain structural features and perhaps lagged behind in others. The lower members of the Jungermanniales have well-developed capsules in the sporophytic phase but exceedingly simple thalli in the gametophytic phase. The higher Jungermanniales have developed elaborate form in the thalli but little differentiation of tissue in these structures. The development in the Marchantiales has been toward differentiation of tissue in the thalli. With the differentiation of tissue in the thalli of the members of the Marchantiales are associated relatively simple sporophytic structures. While the true mosses have developed both advanced gametophytic and sporophytic structures, *Sphagnum* has retained an extremely simple liverwort type of thallus.

The origin of bryophytes is obscure, but it is probable that they evolved from some algal stock. A few fossil bryophytes have been found in Paleozoic rocks and there is evidence that the lines of liverworts and mosses have been distinct since Carboniferous times. Fossil bryophytes have been found in the rocks of the Pliocene epoch of the Tertiary period and from recent glacial deposits. Many of these fossil forms indicate close relationship with living liverworts and mosses. The Bryophyta appear to occupy a position somewhere between the algae and the vascular plants with little evidence of close relationship to either group. The development of multicellular sex organs, especially the archegonium, suggests a position closer to the vascular plants than to the algae. The division Bryophyta, as a group, may perhaps be best considered as divergent from the main phylogenetic line, and it seems unlikely that any group of living bryophytes can be regarded as ancestors of any of the vascular plants.

ALTERNATION OF GENERATIONS

Sporophytic and Gametophytic Generations. In discussing the life histories of plants, it is helpful to keep distinctly in mind that the life

history is an account of events over a period of time. An account of the complete life history of a plant includes all its behavior from the occurrence of a given event in the life cycle through all the various stages to the repetition of this event. Events repeat themselves in the history of organisms. In referring to a phase or a stage of an organism, a certain period of the complete time making up the life cycle is meant. Generally, in animals and in plants a generation is the term applied to the group of offspring of the organism. In plants, however, the term "generation" is sometimes applied to only a certain portion of the complete life history. In fact, one of the most notable features of the life histories of plants is the almost universal occurrence of two alternating phases or generations that differ in many features. They are contrasted in size, in appearance, and in cell features, particularly as to differing chromosome numbers. All plants with sexual reproduction show these two different phases or generations which appear to alternate more or less regularly with each other. There is a production of gametes by one of these generations and the structures produced during this phase comprise the gametophyte, or gamete-bearing plant. The other generation produces the spores, and its structures constitute the sporophyte, or spore-producing plant.

Relative Extent of Sporophyte and Gametophyte. Plants of the various groups differ greatly in the proportion of the total time of their life histories that is occupied by the two different phases. Likewise they vary greatly in the amount and relative conspicuousness of the structures developed in each of the two phases or generations. In general, in the lower groups of plants, the structures of the gametophyte are the more conspicuous features of the life history, and the plant passes most of its life cycle in the gametophytic phase. This is especially true of some of the algae and the bryophytes. In the plants of these groups the sporophytic structures usually are relatively small, inconspicuous, and of short duration, as compared with those of the gametophytic generations. In many of the algae, however, the two alternating generations are independent plants that are often evenly balanced as to size and conspicuousness.

When the higher groups of plants are studied, it becomes evident that the generations are coming to be more evenly balanced, but with a pronounced tendency for the gametophyte to become the less conspicuous and the sporophyte the more conspicuous structure. This is especially true of the ferns and the seed plants. In both of these groups the gametophytic structures are of relatively short duration when compared with the sporophyte.

The life histories of the seed plants show a complete reversal of the situation as shown in the bryophytes. In seed plants, the sporophytic structures are the conspicuous parts of the plant life history. In these

forms, the entire plant (flowering plants, trees, etc.) represents the sporophyte, and the gametophytic structures are reduced to microscopic proportions. The gametophytes of the seed plants are represented by the pollen tubes and the embryo sacs.

Relative Independence of Sporophyte and Gametophyte. As the various groups are considered, there is a change observed in relative prominence of the gametophytic and sporophytic structures. In the lower groups, the algae and the bryophytes, the gametophytic structures are provided with chlorophyll and manufacture their own carbohydrate food and are, therefore, capable of an entirely independent existence. They are also independent as regards the absorption of inorganic substances. In most algae, these inorganic substances are absorbed directly from the water which is the growing medium for these forms. This is also true in the case of some of the bryophytes, although some of the plants frequently have rhizoids which may act as the absorbing structures. The sporophytic structures in these groups are small and are more or less dependent for all food upon the gametophytic thallus. In the higher members of the bryophytes, however, the sporophytic structures develop chlorophyll and become at least partially independent. In all bryophytes, the sporophyte is, nevertheless, dependent upon the gametophyte for the water and inorganic substances, but in the vascular plants the sporophyte is an independent plant. Both gametophyte and sporophyte lead an entirely independent existence in their adult condition in the common ferns, but in heterosporous forms the male gametophytes, at least, are entirely dependent upon the stored food in the spore; the female gametophytes are small and, although chlorophyllose, in most cases probably do not synthesize much carbohydrate food. In seed plants the sporophyte is exceedingly complex and well developed and leads an entirely independent existence, while the gametophyte is only a few cells in extent and consists of structures which, although complex in their morphological homologies, are in all cases entirely dependent upon the sporophytic structures and entirely without chlorophyll.

Nuclear Differences in Sporophyte and Gametophyte. As early as 1894, Strasburger made the generalization that, for plants showing alternation of generations, the generations differ in nuclear constitution. As previously pointed out, this difference lies in the fact that the nuclei of all cells of the sporophytic generation contain twice the number of chromosomes present in the nuclei of the cells of the gametophytic generation. The sporophytic generation is initiated by fertilization, or syngamy, which is the fusion of two $1N$ gametes, resulting in the formation of the zygote, which is $2N$. The zygote is thus the first cell of the sporophyte. It may be the only $2N$ structure formed, as in many of the algae, or it may,

by repeated mitotic divisions, develop into a complex plant body with roots, stems, and leaves, forming the conspicuous plant in the life cycle, as in all vascular plants. No matter how complex the structures resulting from the development of the zygote may be, their cells are all $2N$. Sooner or later, in the reproductive bodies (sporangia) of the sporophyte (or in the zygote if no further development of the zygote occurs) meiosis takes place, whereby the chromosome number is reduced by half ($1N$) in the formation of meiospores. This marks the end of the sporophytic generation and the beginning of the gametophytic generation. The meiospore is thus the first cell of the gametophyte. Its germination and further growth result in the development of the gametophyte. The gametophyte may develop into an independent plant, becoming the conspicuous plant in the life cycle, as in bryophytes, or it may be a very inconspicuous structure consisting of only a few cells and be wholly dependent upon the sporophyte, as in seed plants. In either case, its cells are all $1N$. Sooner or later the gametophyte produces gametes, which on fusion result in the formation of a new sporophyte. The two critical points in the life of plants are therefore **syngamy**, or **fertilization**, and **meiosis**, two compensating processes that keep the numbers of chromosomes in equilibrium through the generations.





CHAPTER 17

TRACHEOPHYTA—THE VASCULAR PLANTS

THE LOWER GROUPS

The development of a vascular system with xylem and phloem tissues is regarded as one of the greatest advances in the evolution of the plant kingdom. Not only is it a structural development but it is of physiological and ecological significance. It is correlated with the ability of plants to live in a terrestrial habitat. The most primitive group of plants with a vascular system is also the most primitive one that can definitely be characterized as land inhabiting.

In recognition of the importance of the origin and development of the vascular system, a grouping of plants has been proposed on the basis of the presence of a vascular system. **Division III, Tracheophyta**—coordinate with division I, Thallophyta, and division II, Bryophyta—is the name suggested for this group. This division includes all vascular plants living and fossil of whatever degree of development; the ferns, lycopods, horse-tails, conifers, flowering plants, and others are placed here. Briefly, Tracheophyta include all plants from the older designations pteridophytes and spermatophytes. The group is one of great biological and economic importance.

CLASSIFICATION OF THE TRACHEOPHYTA

Associated in the division are four subordinate lines, or subdivisions, the **Psilopsida**, the **Sphenopsida**, the **Lycopsida**, and the **Pteropsida**, which are differentiated by variations in their anatomical structures and other morphological characteristics. The ending *-opsida* in these terms is derived from the Greek word *opsis*, meaning "appearance" or "aspect," and these lines include plants from all geological ages that have similar appearance. In the Psilopsida are included all plants that resemble the living plant *Psilotum*. The Lycopsida include plants that resemble the living plant *Lycopodium*. The term Sphenopsida is made up of *sphen*, from the Greek word *spheno*, meaning "wedge," combined with *-opsida*. The Sphenopsida include all plants resembling a fossil form, *Sphenophyllum*, that had wedge-shaped leaves. Similarly, the term Pteropsida, derived from a combination of *pteron*, meaning "feather," and *-opsida*, literally

means "having the appearance or aspect of a feather." The description "feather-like" has been applied to fern leaves. The term Pteropsida, therefore, designates the line that contains all the ferns. Besides the ferns it includes all the higher seed-producing plants. These resemble ferns in their essential morphological and structural features.

In addition to the lines Psilopsida, Sphenopsida, Lycopsidea, and Pteropsida, a more general classification is sometimes found useful. In this classification, classes and orders of plants belonging to the Tracheophyta are separated into two groups, the spore-producing members designated as the **lower vascular plants**, contrasted with the seed-producing members, the **higher vascular plants**.

Within the division Tracheophyta, subdivisions, classes, numerous orders, families, genera, and species are recognized. The reader is referred to pages 328 to 335 where these, with other groups, are coordinately listed. In this chapter only those members of the Tracheophyta not producing seeds, the lower vascular plants, are considered. The following brief classification may serve to show the relative positions of the groups.

THE LOWER VASCULAR PLANTS

The Psilopsida. The Psilotum-like plants.

Order Psilophytales. The oldest known vascular plants from the Silurian and Devonian periods. All forms now extinct.

Order Psilotales. Two living genera resembling the fossil Psilophytales.

The Sphenopsida. The plants with wedge-shaped leaves and similar forms.

Order Calamitales. A group of giant tree forms that were prominent features of the Carboniferous forests. All forms extinct.

Order Sphenophyllales. Small fossil plants with wedge-shaped leaves from the Paleozoic age.

Order Equisetales. A group of generally small living plants also represented in fossils by very large forms.

The Lycopsidea. The lycopods or Lycopodium-like plants.

Order Lepidodendrales. Flourished as tree forms in the Carboniferous forests. All forms now extinct.

Order Lycopodiales. With only two living genera that, although the members are small plants, are representative of a group of fossil plants extending back to the tree forms of the Paleozoic age.

Order Selaginellales. A group of relatively small living plants included in a single genus with numerous tropical, subtropical, and temperate species. In many ways these plants resemble the fossil Lepidodendrales.

The Pteropsida. The fern and fern-like plants.

Class Filicinae.

Order Filicales. The common ferns with many living genera with ancestral types found as fossils in the Mesozoic age and extending back into the Carboniferous period of the Paleozoic age.

Order Ophioglossales. Living fern-like plants.

THE HIGHER VASCULAR PLANTS

The Pteropsida.

Class Gymnospermae.

Class Angiospermae.

These groups of higher vascular plants, containing both living and fossil members, are also included in the Pteropsida. They are considered in this and in the following chapter.

THE RELATIVE SIZE AND IMPORTANCE OF THE GAMETOPHYTE AND THE SPOROPHYTE

As in many lower plants, the complete life cycle of all members of the Tracheophyta consists of two distinct but equally important parts, the gametophytic and sporophytic phases. With widely diversified vegetative forms and various methods of reproduction which are developed during the phases of the life cycles, *the members of the Tracheophyta have one important structural feature in common, i.e., the presence of highly differentiated conducting cells* which are developed during the diploid phase of the life cycle. In the bryophytes and many of the green algae, a macroscopic, physiologically independent $1N$ gametophyte is the most prominent structure developed during the life cycle and is the recognized "plant." In most of these lower forms, the $2N$ sporophyte is physiologically dependent, generally of small size, and inconspicuous; in some cases it is even of microscopic proportions. In contrast, the structures developed during the $2N$, or sporophytic, phase of all members of the Tracheophyta are more prominent and live longer than those of the $1N$, or gametophytic, stage. The diploid sporophyte is the recognized plant body of all Tracheophyta with the haploid gametophytic thallus relatively small, of simple structure and, in the higher forms, restricted to microscopic proportions. The sporophyte of the Tracheophyta generally is differentiated into true roots, stems, and leaves with well-developed vascular, or conducting, tissue throughout all plant parts. Some primitive members of the group, however, may lack roots and well-developed leaves. In all cases, the sporophyte, as its name indicates, produces sporangia and meiospores that are $1N$ structures developed as a result of meiosis.

Regardless of the differences in size and structural complexities, the physiologically independent $2N$ sporophytes of the Tracheophyta are comparable with the physiologically dependent diploid sporophyte of the bryophytes. Both originate at fertilization and develop from the zygote. Both develop sporocytes that undergo meiosis and eventually produce meiospores. Likewise, the $1N$ gametophytes of bryophytes and Tracheophyta are comparable. Both originate in a similar manner, *i.e.*, during meiosis, and they develop from germinating meiospores. The gametophytes in each group produce gametes.

THE PTEROPSIDA

The Pteropsida, which include all living and fossil ferns and which extend beyond the limits of the older group of the pteridophytes to include all the seed plants, comprise the largest and most important of plant groups. The pteropsid line, as are the others, is distinguished by specific morphological and anatomical features. A wide range of vascular stele types is found in the Pteropsida. In the plants composing the Pteropsida, there are protosteles and all types of siphonosteles. Some of these have mesarch and others endarch xylem. These diversities in anatomical structure all occur in the ferns. Siphonosteles with endarch xylem are characteristic of all higher vascular plants. In general, the Pteropsida have large leaves, which, in most ferns especially, are a prominent feature. In the higher members of the Pteropsida, while the leaves may not be conspicuously large, they are generally well developed. **Leaf gaps, or breaks in the vascular cylinder, are a characteristic feature of the stem anatomy** (pages 183 to 184 and Fig. 233). Sporangia are borne on the under, or abaxial, surface of unmodified and modified leaves or sporophylls.

Among the classes and orders of the living Pteropsida are the following:
Class Filicinae. The ferns and fern-like plants.

Order Filicales. The true ferns. Genera *Polypodium*, *Pteris*, *Marsilea*, etc.

Order Ophioglossales. The adder's-tongue and grape ferns. Genera *Ophioglossum* and *Botrychium*.

Fossil Forms. The fossilized remains of many extinct types of ferns are known.

CLASS FILICINAE—THE FERNS AND FERN-LIKE PLANTS

ORDER FILICALES—FERNS

The order Filicales includes the common land-inhabiting ferns which are widely distributed and well known in both tropical and temperate regions. The sporophyte, the conspicuous phase of the life cycle, is a perennial plant. In contrast, the gametophyte, a small thallus structure, is usually of short duration and disintegrates soon after the sporophyte, which arises from it, becomes an independent plant. Unless attention is directed to the gametophytes, they usually escape the attention of the casual observer. All the common ferns *produce a single type of spore*; they are therefore said to be **homosporous**. Associated with the common ferns is a group of diversified plants called the "water ferns." All of these produce *two kinds of spores*, some large ones and others very much smaller; they are said to be **heterosporous**. Since the sporophyte is the conspicuous plant in the life cycle, it is discussed first.

The ferns are widely distributed, occurring in both temperate and

tropical regions. It is in the tropics, however, that they attain their greatest development. The wealth of species and luxuriousness of growth of these plants in the tropics are not even closely approached in temperate



FIG. 229. *Alsophila australis*, one of the tree ferns. (Photograph by courtesy of Conservatories New York Botanical Garden.)

regions. Ferns are generally small or medium-sized plants making up a part of the ground flora in moist forests. The largest living representatives are the "tree ferns" of the tropics that attain heights of 30 to 40 ft. and are conspicuous features of the flora (Fig. 229). In general, the ferns grow in moist terrestrial habitats, but many notable exceptions are found.

Some grow as floating aquatics; some are rooted in mud and may be partially covered with water; others are epiphytes on tree trunks in moist tropical and temperate zone forests (Fig. 230); and still others grow under extremely dry conditions. Some of these xerophytic forms may be found in the crevices of rocks on the sides of vertical cliffs. In such situations they dry out, the leaves curl up, and the plants lie dormant during periods of drought. On the return of more moist conditions, they absorb water and quickly revive.

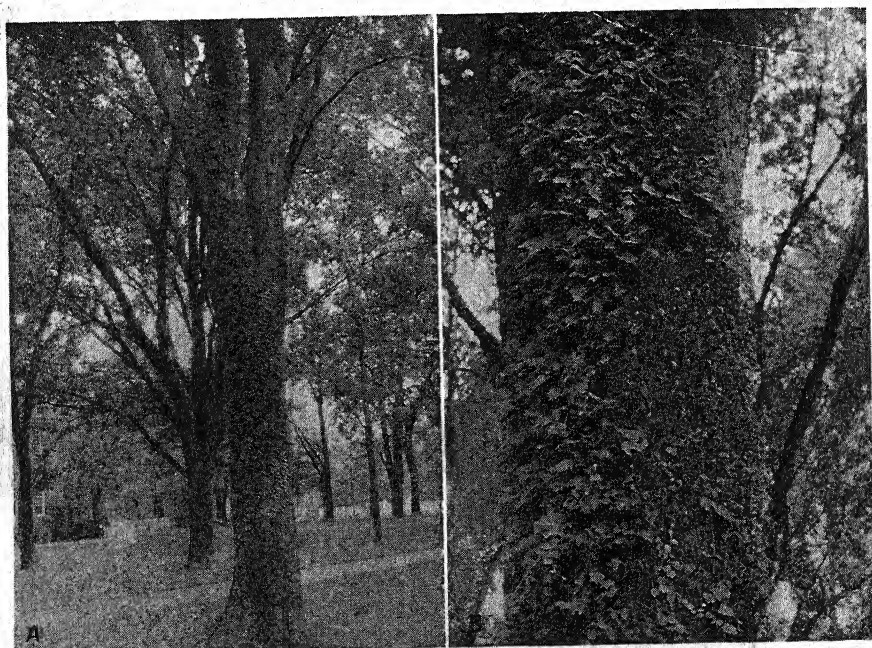


FIG. 230. A, *Polypodium polypodioides*, an epiphytic fern growing on a specimen of American elm on the campus of the college of William and Mary, Williamsburg, Va.; B, close-up view of the same. (Photographs by Frank R. Nivison.)

The Sporophyte. The sporophyte is a diploid, or $2N$, structure. In its early, physiologically dependent stages, it consists of the embryonic root, stem, leaf, and a foot that is attached to the independent gametophyte and functions as an absorbing organ. The mature sporophyte with roots, stem, and leaves bearing sporangia is the recognized fern plant (Fig. 231).

The Stem. The fern stem is generally a small, creeping, underground structure, but sometimes a larger, erect, radial one, showing nodes and internodes somewhat indefinitely. The stems of tree ferns are relatively large structures attaining heights of several feet and diameters of several inches (Fig. 229). The perennial stems of ferns live for many years.

Because of the presence of extremely hard tissues, the old dead portions of the stem often persist for several years longer. Each year the fern stem produces a new group of leaves and sporangia. Conspicuous features of

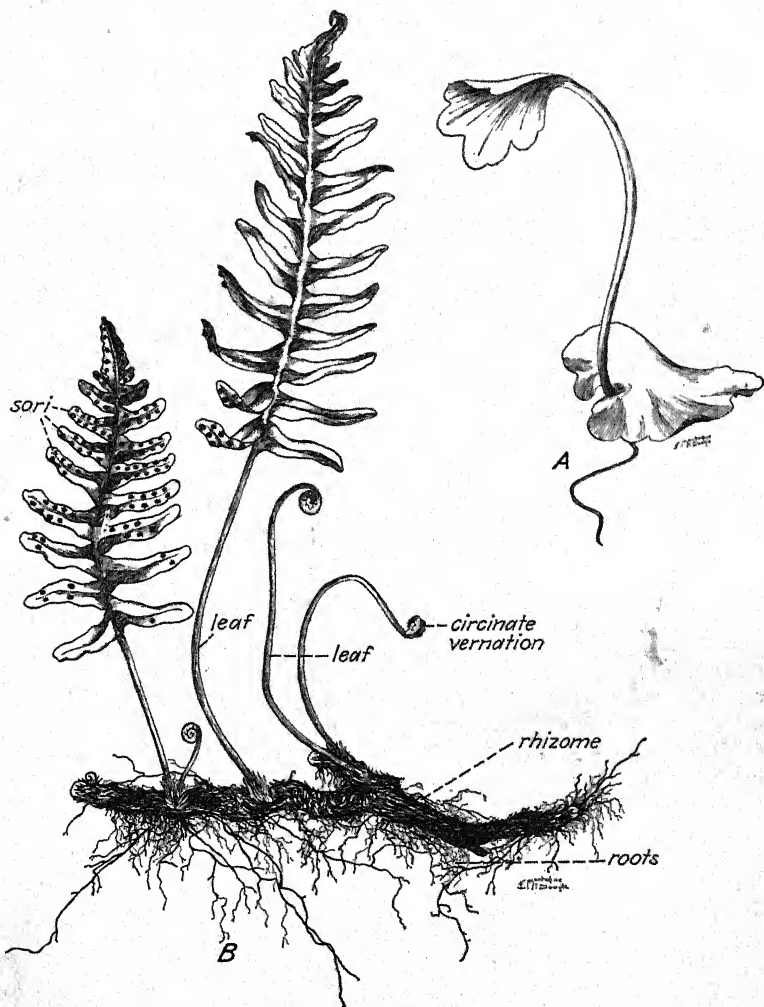


FIG. 231. Habit of fern. A, young sporophyte growing from mature gametophyte; B, mature sporophyte of *Polypodium virginianum*. (Drawings by Elsie M. McDougle.)

the fern stem are the leaf bases, which frequently persist for several years, and a hairy outgrowth called **ramentum**, which covers the younger portions of the stem.

The tissue systems characteristic of plants are clearly delineated in the fern stem (Figs. 83, 232, 233). The epidermis of the fern stem is more permanent than that of the woody dicotyledonous plants. This results from the fact that there is no development of secondary growth in the ferns such as occurs in dicotyledons, and hence no breaking of the epidermis as the stem increases in diameter. The fundamental or ground tissue, cortex and pith, are relatively more abundant than in the dicotyledons and are practically alike. A modification of this tissue which may occur in either cortex or pith is the development of hard and thickened walls which change these cells into a sclerenchymatous tissue (Fig. 232). The development of this sclerenchyma in some species is so extensive that it assumes a greater role in strengthening and support than does the vascular system. This modification is not confined to the stem but extends into roots and leaf petioles.

The vascular tissues, consisting of xylem, or water-conducting and strengthening tissue, and phloem, or food-conducting tissue, are usually bounded by a pericycle, consisting of a few layers of parenchyma cells, and a well-defined endodermis. In many species of ferns there are separate vascular bundles of the concentric type, each surrounded by a pericycle and an endodermis (Figs. 232, 233). The xylem is made up principally of pitted or scalariform tracheids, and the phloem of sieve tubes with sieve plates on the side walls. No cambium is present.

The vascular system of the ferns shows great diversity in structure. The various genera of the order show most of the known types of stelar arrangements, such as the protostele, the amphiphloic siphonostele, the ectophloic siphonostele, and the dictyostele (Figs. 83, 232). Since the anatomy of the fern stem is not complicated by the development of secondary tissues, the primary tissues such as endodermis, pericycle, xylem, phloem, and parenchyma are readily observed in stem sections (Figs. 232, 233).

In the development of the vascular system of a stem, there is a definite manner of differentiation of the xylem tissues, which is an important anatomical feature. It will be recalled that the protoxylem cells are the first xylem cells to be differentiated from the procambium strand and that the metaxylem is the later differentiated primary xylem. Typically, in ferns, the metaxylem differentiates in all directions from the protoxylem points. Therefore, when the primary xylem is mature, the protoxylem is completely surrounded by metaxylem. This type of differentiation is termed the **mesarch** condition, in contrast to the **endarch** condition, in which metaxylem differentiates only outward in a radial direction from the protoxylem, and the **exarch** condition, in which metaxylem differentiates only inward from the protoxylem. The mesarch condition is characteristic of ferns and is further anatomical evidence that their evolutionary position is between the Lycopodiales, which show the exarch condition, and the seed plants, which are endarch.

Another anatomical feature very characteristic of the ferns and of great phylogenetic significance is the presence of leaf gaps in the vascular cylinder of those genera having a siphonostele. When leaves develop, a vascular strand passes from the vascular cylinder of the stem out through the cortex and into the petiole of the leaf. Such a strand is called a **leaf trace**. At the region of the vascular cylinder of the stem where the vascular connections to the leaf come away from it, a break occurs in the continuity of the cylinder. This break is called a **leaf gap**. Leaf gaps are characteristic of ferns, gymnosperms, and angiosperms, which collectively make up the Pteropsida, in contrast to the Lycopsidea, composed of the Lycopodiales, including the fossil representatives of this group, which do not have leaf gaps.

The Root. The roots of ferns are generally small, wiry structures which grow from the stem and penetrate the soil (Fig. 231). They

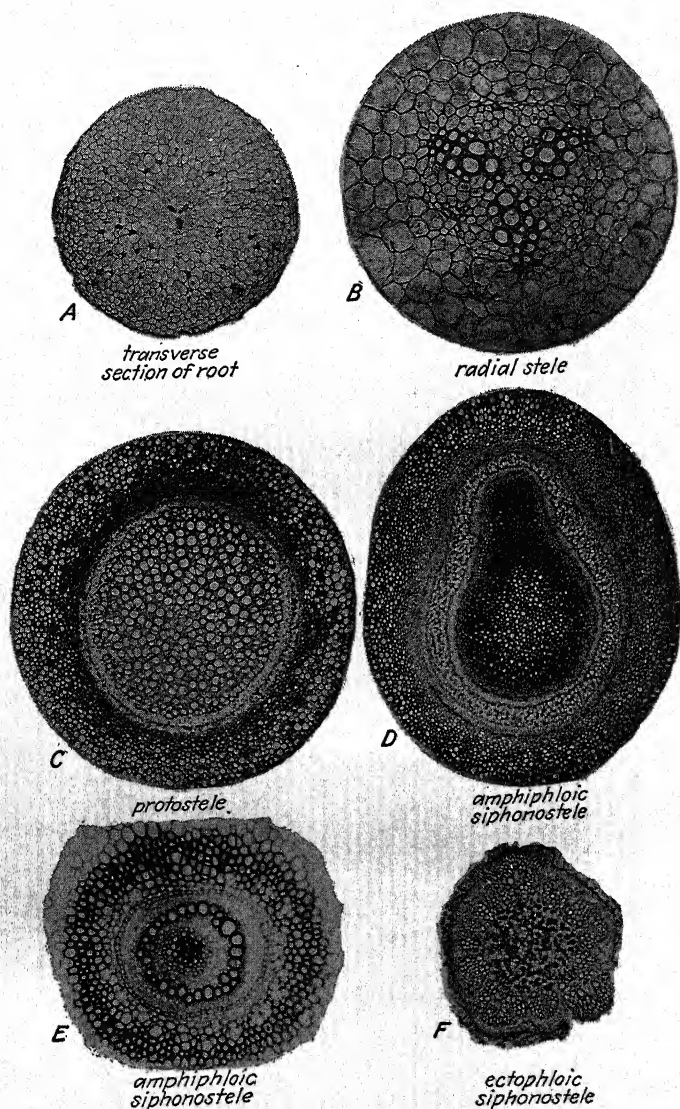


FIG. 232. Anatomy of ferns. A, transverse section of the root of *Botrychium*, showing radial stele in the center surrounded by endodermis, cortex, and finally epidermis on the outside; B, enlarged view of transverse section of the radial stele of *Botrychium*; C, transverse section of protostele of *Gleichenia*, a tropical fern; xylem in the center surrounded by cylinder of phloem; D, transverse section of the amphiphloic siphonostele of *Adiantum*, showing a cylinder of xylem with phloem and endodermis both inside and outside the xylem, and parenchyma occupying the center of the structure; E, transverse section of the amphiphloic siphonostele of *Marsilea*; structure similar to that of D; F, transverse section of ectophloic siphonostele of *Osmunda*; xylem cylinder with the phloem on the outside only; parenchyma occupies the outside of the structure; D and E show sclerenchyma cells in the parenchyma regions.

are frequently very abundant, forming a mass around the horizontal underground stems. The same tissue systems occur in roots as are developed in stems, the epidermal, the fundamental, and the vascular (Figs. 232, 233). The detailed anatomical features of roots of ferns are very similar to the primary structures generally occurring in the roots of all plants. The vascular cylinder has typically the exarch, radial arrangement of the xylem and phloem.

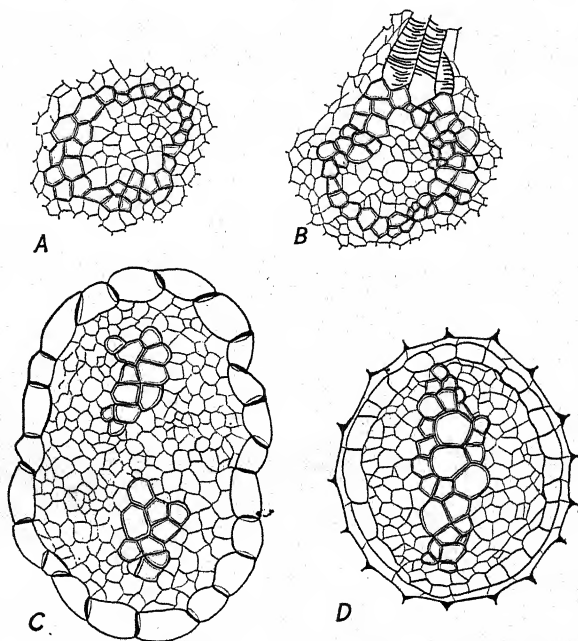


FIG. 233. Vascular structures of ferns. A, transverse section of portion of stem of young *Pteris* sporophyte, showing stage in development characterized by a siphonostele; heavy-walled cells are xylem; B, stage similar to A but showing root developing; C, *Botrychium*, transverse section of portion of root, showing the diarch condition; heavy-walled cells at each end are the xylem; endodermis conspicuous on outside; D, *Polypodium*, transverse section through portion of the stem, showing one of the bundles of the dictyostele; xylem in center surrounded by phloem and parenchyma cells.

The Leaf. The leaves of common ferns are quite variable in size and form but are all characterized by circinate vernation, as can be seen by an examination of their growing tips (Figs. 231, 235). Simple leaves are present in some species, as in the walking fern (*Camptosorus*) (Fig. 234, F), but in most species the leaves are compound—most often once compound, sometimes twice or three times compound. The Boston fern, for example, except for some of its recent modified forms, has leaves that are once compound, *i.e.*, pinnately compound. The leaflets are known as

pinnae. In such ferns as the cinnamon fern or the maidenhair fern, the pinnae are also compound, and their ultimate divisions are known as **pinnules**. In size, fern leaves are equally variable. The walking fern (Fig. 234, *F*), for example, has leaves but a few inches long. At the other extreme are leaves of giant size, sometimes as much as 6 ft. in length (Fig. 229). As would be expected, such large leaves are usually compound.

The structure of fern leaves is similar to that of leaves of higher plants.

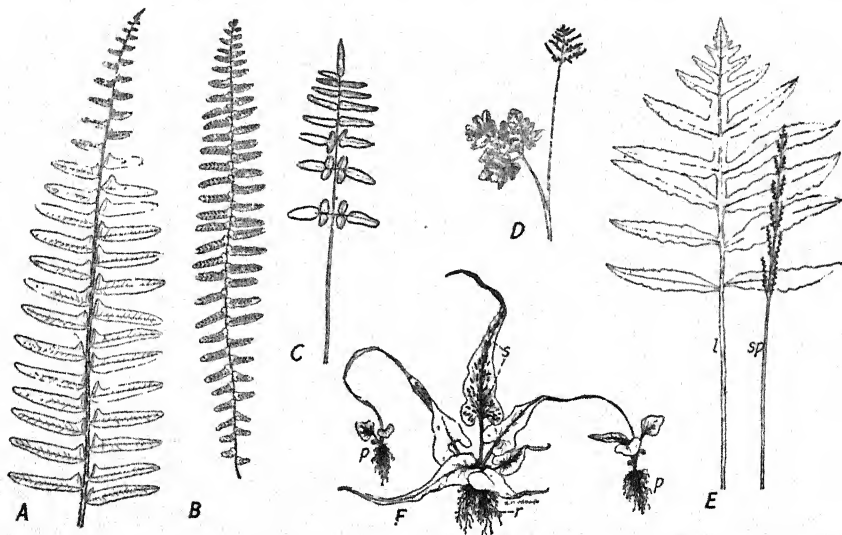


FIG. 234. Types of leaves or sporophylls of ferns. *A*, leaf of the Christmas fern (*Polystichum acrostichoides*), the upper pinnae bearing sori; *B*, leaf of a spleenwort fern (*Asplenium platyneuron*), showing sori on all the pinnae; *C*, leaf of the cliff brake fern (*Pellaea atropurpurea*), the sori continuous around the margin of the pinnae; *D*, leaf of the grape fern (*Botrychium* sp.); with a vegetative leaf and a fertile leaf bearing sori; *E*, foliage leaf, *l*, and sporophyll, *sp*, of the sensitive fern (*Onoclea sensibilis*); *F*, walking fern (*Camptosorus rhizophyllus*), showing asexual reproduction by turning down of leaf tips which give rise to new plants, *p*; sori on leaves, *s*; roots, *r*. (*A-E*, drawn by Edna Stamy Fox; *F*, by Elsie M. McDougle.)

There is a well-developed epidermal layer with stomata that are usually confined to the lower surface. Guard cells with chlorophyll occur as in higher plants (Fig. 236). Internally, the differentiation of the mesophyll into a palisade region and a spongy region is usually evident, but these regions are not sharply marked in ferns that live mostly in shaded habitats. The vascular system of the leaves is not materially different from that of the stems. The venation, however, is peculiar in that the larger veins are in many instances dichotomously branched. Generally, the vascular bundles of the larger veins are concentric or bicollateral, while those of the smaller veins are of the collateral type.

Vegetative Leaves and Sporophylls. In many of the ferns, the sporangia, or spore cases, are produced on the underside of the ordinary vegetative leaves. Examples of this condition are seen in the maidenhair fern

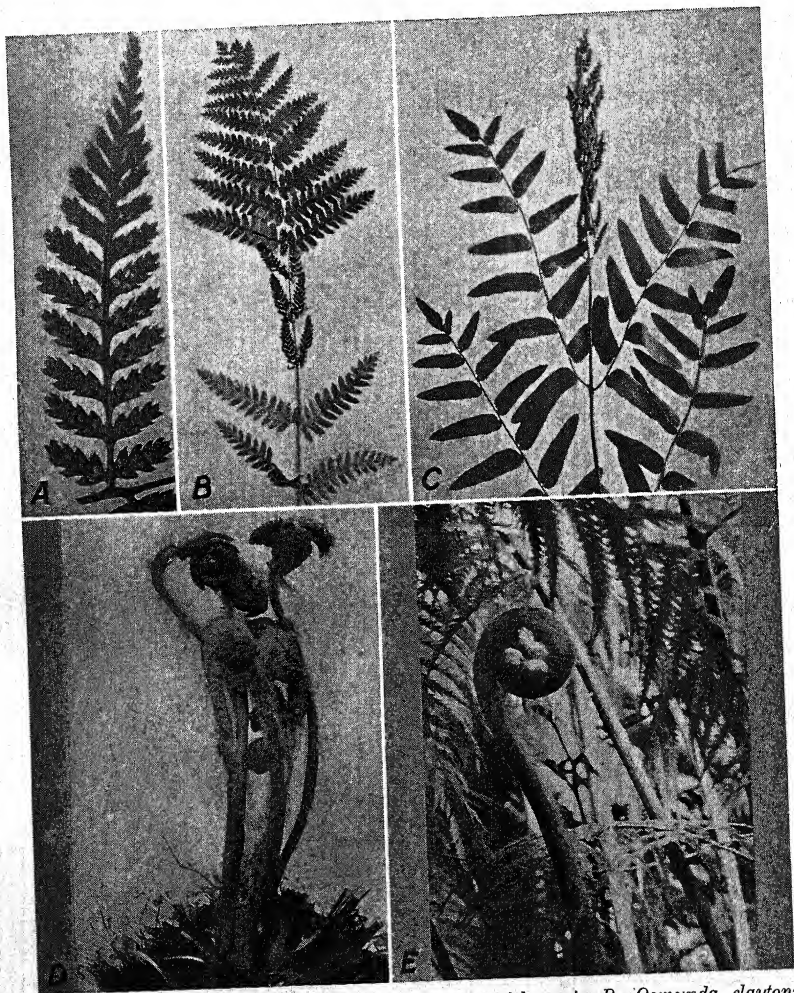


FIG. 235. Fern-leaf types. A, *Dryopteris spinulosa* with sori; B, *Osmunda claytoniana*, vegetative leaf interrupted by groups of fertile leaflets; C, *Osmunda regalis*, fertile leaflets, terminal; D, *Osmunda* sp., illustrating circinate vernation of leaves; E, portion of Schiede's tree fern (*Cibotum Schiede*), showing characteristic vernation. (E, photograph by courtesy of Conservatories, New York Botanical Garden.)

(Fig. 237, E). In some genera, such as the royal fern and the Clayton fern, sporangia are borne on special modified portions of the foliage leaves (Figs. 234, 235). In the Clayton fern, several segments near the middle

of the leaf bear all the sporangia and are quite different in appearance from the sterile segments in that they contain no chlorophyll and are considerably contracted in size. In other genera, as in the sensitive fern, the sporangia are produced on leaves that are wholly modified and so are distinctly different in appearance. Any leaf bearing sporangia is called a sporophyll regardless of the amount of modification in its structure.

In the genera in which the sporangia are produced on the ordinary vegetative leaf, the leaf has a double function, that connected with the metabolic activities of the plant and that as a spore-producing member or sporophyll. In the genera with sporophylls and vegetative leaves distinct, the sporophylls generally have no function other than that of

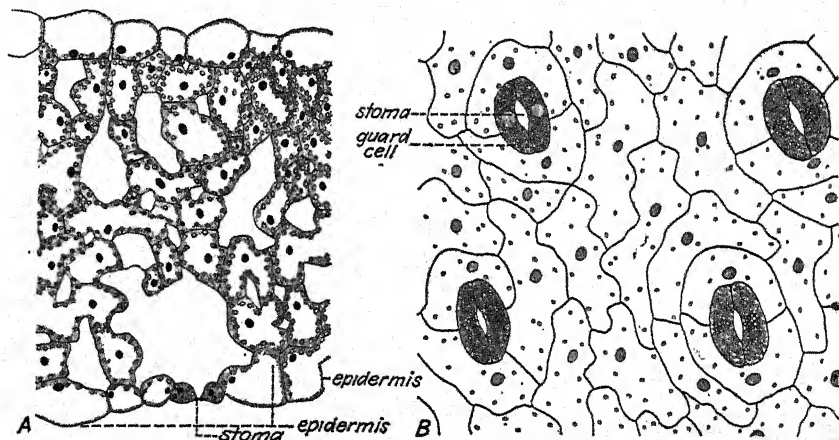


FIG. 236. Details of leaf structure of ferns. A, *Pteris*, cross section showing structure; B, *Nephrolepis*, surface view of lower epidermis showing stomata.

spore production. They usually lack chlorophyll and have thus no photosynthetic function. In cases in which there are two kinds of leaves, sterile vegetative leaves and fertile spore-bearing leaves, the plant is said to show dimorphism in its leaves.

The Sporangia and the Sori. The sporangia of ferns show almost every conceivable manner of distribution over the surfaces of the leaves (Fig. 237). Much of the classification of ferns into families and genera is based upon the manner of distribution of the sporangia. In certain fossil ferns and in some primitive living ferns, they are grouped around a central receptacle, and in some instances several of these sporangia grow upon a single common stalk. In some living ferns of primitive types such as *Marattia*, the sporangia are united laterally, forming a compound structure termed a **synangium**. The synangium is an elongated structure generally paralleling an underlying vein.

In general, the sporangia occur on the underside of the leaf surface (Fig. 237). Their distribution varies from an irregular arrangement covering patches of the under leaf surface, or sometimes entirely covering the undersurface of the sporophylls, to conditions in which a single sporangium occurs distinct from all others. When the sporangia are grouped, as they frequently are, the group is termed a *sorus* (plural *sori*). In

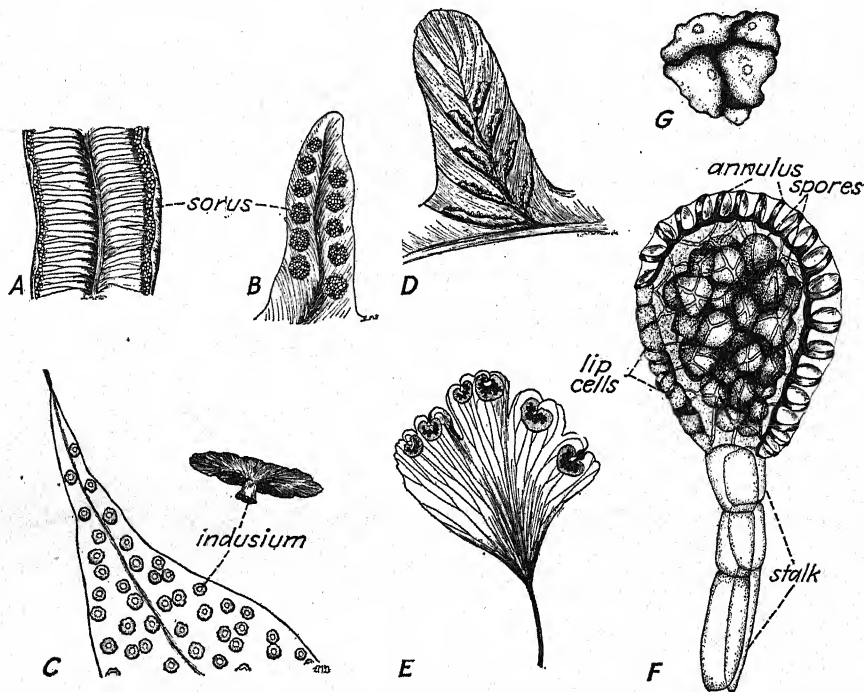


FIG. 237. Fern sori and sporangia. A, portion of pinna of a species of *Pteris*, the brake fern, showing the false indusium covering the marginal sporangia; B, sori of *Polypodium vulgare*, the polypody fern, without indusia; C, portion of pinna and a single detached indusium of *Cyrtomium falcatum*, the holly fern; D, pinna of *Asplenium* sp., one of the spleenwort ferns, showing the indusia attached along the margins of the sori; E, pinnule of *Adiantum pedatum*, the maidenhair fern, with marginal sori covered by false indusia; F, a single sporangium; G, a tetrad of four spores. (Drawing by Elsie M. McDougale.)

general, the sori have definite positions on the leaf surface, being usually found on the veins or at vein endings, the location being related to their nutrition. Frequently, sori occupy a marginal position on the leaf. In some ferns, as in the genus *Pteris*, in which the sporangia occupy a marginal position on the underside of the leaf, with no distinct sori, the situation is described as "sori confluent." Not only are the sori of rather definite position but also of definite shape, the shape varying from round, kidney-shaped, or reniform, to elongate or crescent-shaped. In addition,

the sorus is frequently protected by a definite covering called an **indusium**. This is a thin membranous tissue attached in some way to the leaf surface and covering the sporangia, at least during the period of their development. The indusium is regarded as a part of the sorus. While the indusium is a structure common to the fern sorus, it is by no means universal. There are several genera of ferns in which the sporangia develop without the protection of an indusium. In others, as in the genus *Pteris*, the sporangia are protected by the reflexed margin of the leaf, which is folded backward (under) and provides an efficient covering for the developing sporangia. This type of covering is called a "false indusium."

Two types of sporangial development occur among the ferns. In one a single superficial cell of the sporophyll divides into an outer and an inner cell. The wall of the sporangium develops from the outer of these two cells and the sporogenous tissue from the inner one. This is the **eusporangiate** type of development. It is characteristic of most vascular plants, including the primitive *Marattia* and the Ophioglossales. The common ferns are unique in their contrasting sporangial development, the **leptosporangiate** type. Their sporangia develop entirely from the outer portion of a single superficial initial cell of the sporophyll (Fig. 238). The initial cell divides, forming a transverse wall parallel to the surface of the sporophyll. The inner cell takes no further part in the development and its identity is eventually lost. By a series of divisions, the outer cell forms the sporangium, including the stalk, the wall, and the inner spore-bearing tissue.

In the young developing sporangium, there is a large triangular cell called the **central cell**. By a series of divisions in the central cell, there is differentiated a layer of nutritive tissue, called the **tapetum**, surrounding the primary sporogenous cell (Fig. 238, *F*). By four successive mitotic divisions, the primary sporogenous cell forms typically 16 spore mother cells, or sporocytes. Each of the diploid sporocytes eventually undergoes meiosis and forms a quartet of haploid meiospores, which are the first cells of the new gametophytic phase of the fern. As the sporangium enlarges and develops, the walls of the tapetal cells disintegrate and their cytoplasmic contents and nuclei form a nourishing medium for the sporocytes and spores. The dependence of the early gametophytic cells upon the old sporophyte for nutrition is evident, since the tapetum and the sporangium as well as the entire fern plant are sporophytic structures.

While the spores are maturing, the rest of the sporangium continues its development. The stalk, developing at the base, elongates and elevates the spore case from the surface of the sporophyll. The mature sporangium consists of a slender **stalk**, attaching it to the tissues of the sporophyll, and a **capsule**, or **spore case**, that contains the spores. The wall of the spo-

rangium is one cell layer in thickness. The wall is modified to form the **annulus**, or organ of dehiscence, and the **stomium**, a structure of specialized cells, sometimes called the **lip cells**, permitting an easy cleavage when the sporangium begins to dehisce (Fig. 237, *F*). The annulus consists of a single external row of specially thickened cells usually extending vertically from the stomium and encircling the capsule. There are, however, many variations in the structure and position of the annulus. The stomium is located on one side of the sporangium, and, when opened, starts a transverse break in the wall of the capsule. The walls of these cells are all greatly thickened except those exposed to the exterior. The annulus and

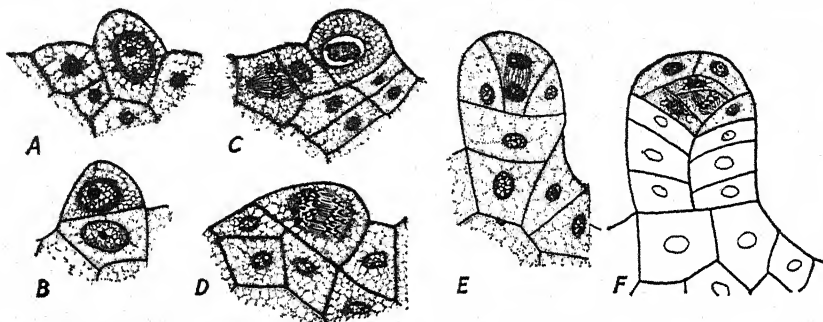


FIG. 238. Early stages in development of sporangia of ferns. *A*, initial cell of the sporangium just protruding above the surface; *B*, the basal cell has been cut off; *C* and *D*, stages in division; *D*, showing anaphase of division which will result in the development of a vertical wall as shown in *E*; *E*, young sporangium with basal cell and three curved vertical walls, two of which are shown in drawing and one of which is in the plane of the page; the central cell which is pyramidal in shape is now known as the apical cell of the sporangium; the division figure in the apical cell is the division to form a cell from which is developed the upper part of the wall as shown in *F*; *F*, the central cell dividing to complete the formation of the three primary tapetal cells.

stomium constitute the opening mechanism of the capsule, which is one of the most interesting structures evolved by plants. During the final maturation of the sporangia, the cells of the annulus lose water as the walls of the sporangia begin to dry. The water remaining within the cells is held by a strong cohesive force which causes the thin outer walls to be drawn inward. The thicker side walls are thus drawn together, shortening the outer circumference and causing the annulus to be gradually pulled backward on itself, away from the stomium. The capsule thus slowly opens at the stomium or lip. The line of dehiscence is extended transversely across the sporangium, breaking the cells of the side walls, which are very thin and delicate. The annulus, carrying the spores with it, continues to bend backward and is held under greater and greater tension as the cells dry out, until eventually the cohesive force of the water is over-

come, when the annulus suddenly snaps back into its original position and by this motion forcibly ejects the spores.¹

The Gametophyte. Upon germination, the spores produce, at first, a short filament of cells resembling a green alga or a moss protonema. Further development of these structures varies considerably in the different genera and according to light and temperature conditions. There are fern gametophytes which continue in the filamentous condition even to maturity, but the typical mature fern gametophyte is a small, flat, heart-shaped thallus, $\frac{1}{8}$ to $\frac{1}{3}$ in. in diameter (Fig. 239). The amount of light

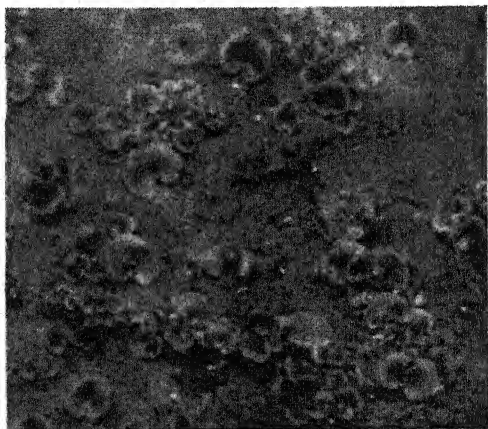


FIG. 239. Fern prothallia on soil.

determines very largely the exact shape. When light is strong, the heart-shaped thallus, or cordate type, soon replaces the filamentous condition.

The thallus of cordate shape is developed by the repeated divisions of a wedge-shaped apical cell which is formed at the end of the filament resulting from the germination of the spore (Fig. 240). The apical cell divides, cutting off alternate segments to right and left. These segments, by further transverse divisions, form the vegetative cells of the thallus. The lobed or heart-shaped condition is thus attained by the rapid growth of the segments cut off from the apical cell. This growth of the segments is more rapid than that of the apical cell, and the lobes consequently tend to over-

¹ The opening of the capsule can be demonstrated by placing unopened ripe sporangia in a drop of glycerin on a slide and observing without a cover glass under a microscope. The glycerin slowly removes the water from the cells of the annulus by osmosis. The annulus then behaves in a manner analogous to that in nature. The heavy liquid (glycerin) retards the snapping motion, which can then be observed readily by the student. The spores are scattered in the drop of glycerin.

grow the apical cell, which therefore comes to occupy a position in the notch of the heart-shaped thallus.

The thallus at maturity is a thin, flat mass of tissue, its lobes consisting of

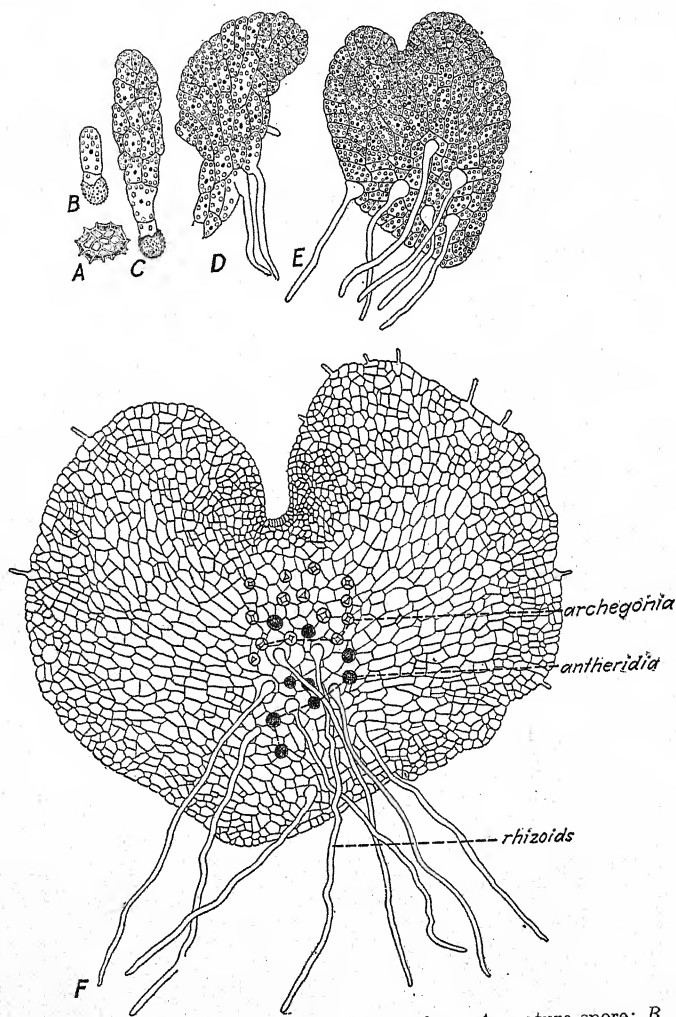


FIG. 240. Stages in development of gametophyte of fern; A, mature spore; B, germinating spore; C-E, developing thalli; F, mature thallus.

a single layer of cells, while the central part is more massive, consisting of several layers of cells. On the underside of the thallus, rhizoids are produced which are similar to the rhizoids of the thalli of the liverworts and serve as organs of attachment for the thallus (Fig. 240).

The Sex Organs. The sex organs, the antheridia (male) and the archegonia (female), are produced on the underside of the thallus. Young thalli produce only antheridia, but older thalli produce both antheridia and archegonia. The antheridia are located on the thinner portion of the thallus, often among the rhizoids. The archegonia are produced on the thickened portion of the thallus, just back of the notch in which the apical cell is located.

An outstanding feature of the sex organs of ferns is the reduction of the sterile or unessential tissue, such as the wall cells of the antheridia and the neck cells of the archegonia. The wall of the mature antheridium consists of three cells besides the basal cell: a funnel-shaped cell, a second ring-shaped cell adjacent to it, and the spherical cap cell at the top (Fig. 241, C). This structure might be roughly visualized by placing two hollow rings one above the other and then closing the opening at the top with a spherical ball of the proper size. The enclosed central portion originally consists of a single cell, called the central cell, which is the primary spermatogenous cell. The central cell continues to divide until about 32 spermatogenous cells are formed. The number of spermatogenous cells is sometimes larger, regularly so in the antheridia of the lower or more primitive members of the ferns. The spermatogenous cells separate from each other and float free in a mucilaginous mass. In the actual formation of the sperm, within the spermatocyte, the nucleus forms most of the structure, but a portion of the sperm is developed from the cytoplasm. At maturity, the sperm consists of a nucleus within a spirally coiled body to which are attached many cilia. The antheridium breaks open and the sperms escape by the rupture of the wall, generally the apical or cap cell, or sometimes by the separation of the cap cell from the adjacent ring cell. The actual rupture of the wall is accomplished by the absorption of water by the mucilaginous contents of the antheridium at the time of maturity. The sperms are pushed out by the pressure of the turgid wall cells. At maturity, each is surrounded by a thin vesicle of material composed of the remains of the cytoplasm of the spermatocyte. When shed, the sperm is within a thin membrane which is a portion of the wall of the spermatocyte. This membrane soon dissolves in water, and the sperm is freed. As a swimming structure, it is dependent upon water to achieve contact with the egg in the archegonium.

The mature archegonium of the common fern consists of an enlarged basal portion, or venter, which is deeply sunken in the tissues of the thallus, a very short neck, which is curved backward owing to the unequal growth of the neck cells, and an axial row of normally two neck canal cells, a ventral canal cell, and the egg, or ovum, at the base in the venter (Fig. 241, A). When the egg is ready for fertilization, the neck canal and

ventral canal cells disintegrate, the neck of the archegonium opens, and a portion of the disintegrating neck canal and ventral canal cells is extruded. The remainder of the material forms a fluid through which the sperm may pass to fertilize the egg. The neck is then much like a short hollow tube offering a good clear passage for the sperm to penetrate to the egg. The egg is a single, large, nearly spherical cell with a depression on the side toward the neck of the archegonium. The depressed portion becomes the "receptive spot" which admits the sperm at fertilization.

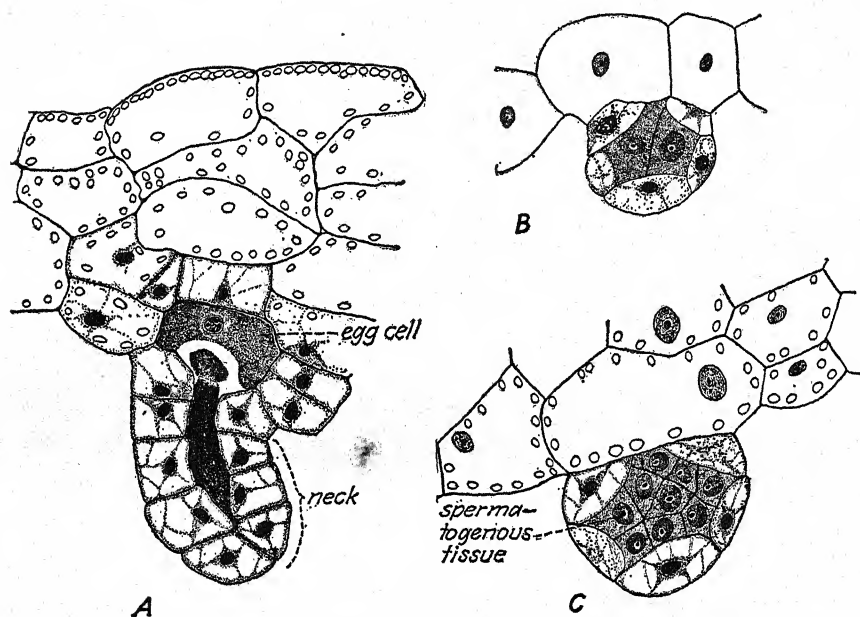


FIG. 241. Sex organs of fern. A, mature archegonium with ventral canal cell and neck canal cells disintegrating; B and C, stages in development of an antheridium.

It has been demonstrated that the sperm is caused to swim to the archegonium by the chemical attraction of certain substances secreted by the archegonium. One of these substances is malic acid, but various organic and inorganic salts formed in the archegonium are known to have possibilities of exerting positive chemotactic stimuli upon the sperms. The sperm enters the neck of the archegonium and advances to the egg by a slow spiral-like motion. It enters the egg at the receptive spot and very slowly the process of fusion of the nucleus of the egg and the nucleus of the sperm is accomplished. With fertilization, the diploid ($2N$) condition of the chromosomes is reestablished and the sporophytic phase begins. Since the gametes are the last haploid structures formed, the

end of the gametophytic phase is marked by the union of these structures. The zygote is the first structure formed in the diploid generation.

The Embryo and Its Development. The embryo and its development constitute the early stages in the development of the sporophyte (Fig. 242). As soon as fertilization is accomplished, the zygote develops a membrane. Segmentation by the ordinary mitotic division takes place, dividing the zygote by a vertical wall into an anterior (front) half and a posterior (back) half. A second transverse division forms four cells, the two anterior ones producing the stem and the first leaf, and the two posterior ones producing the root and the foot. These quadrants develop by rather regular divisions during their early stages. The leaf, stem, and root of the fern embryo have the characteristic features and functions

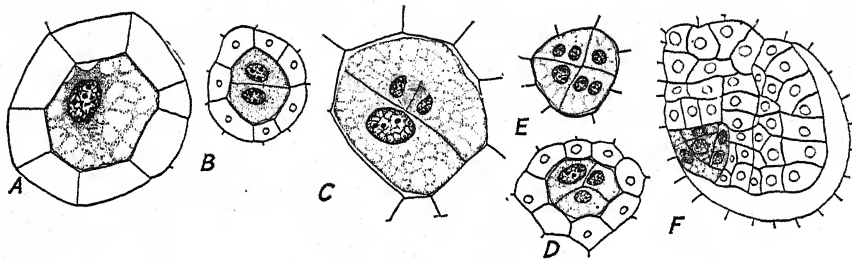


FIG. 242. Early stages in development of the embryo of a fern (*Pteris*). A, fertilized egg; B-E, early stages in growth by cell division; F, somewhat older stage, with apical cell of root differentiated.

of these organs. The foot is, at maturity, a short projecting hemispherical mass of cells in close contact with the cells of the thallus. The foot absorbs nutrients from the gametophyte for the young embryo. In the early stages, the embryo is entirely dependent upon the gametophytic tissues (Fig. 231, A), but soon the root and the leaf of the embryo emerge from the archegonium wall, or calyptra, as that structure is called. With the development of the leaf and the root, the young sporophyte manufactures its own carbohydrate food, absorbs water and mineral matter from the soil, and soon becomes independent of the gametophyte. Growth of the sporophyte is slow from the embryo to the mature fern plant. Most fern plants reach maturity after 2 or 3 years.

The Water Ferns. The water ferns (Hydropteridineae), so named on account of their aquatic habitat, are a small group consisting of but four genera that are considerably different from ordinary ferns. Two of these genera, *Azolla* and *Salvinia*, are floating forms, while the others, *Marsilea* and *Pilularia*, grow rooted in the mud at the bottom of quiet water or on the banks of ponds and sluggish streams. *Azolla* has a very small stem, a few roots, and very small leaves. *Salvinia* is very similar but has larger

leaves. *Pilularia* and *Marsilea* are larger plants made up of roots, stems, and leaves. In appearance, the last two genera look more like grasses or clovers than like ferns. Unlike the common ferns already discussed, the water ferns are **heterosporous**; *i.e.*, they produce two kinds of spores, **microspores** and **megaspores**. The microspores give rise to male gametophytes and the megaspores to female gametophytes.

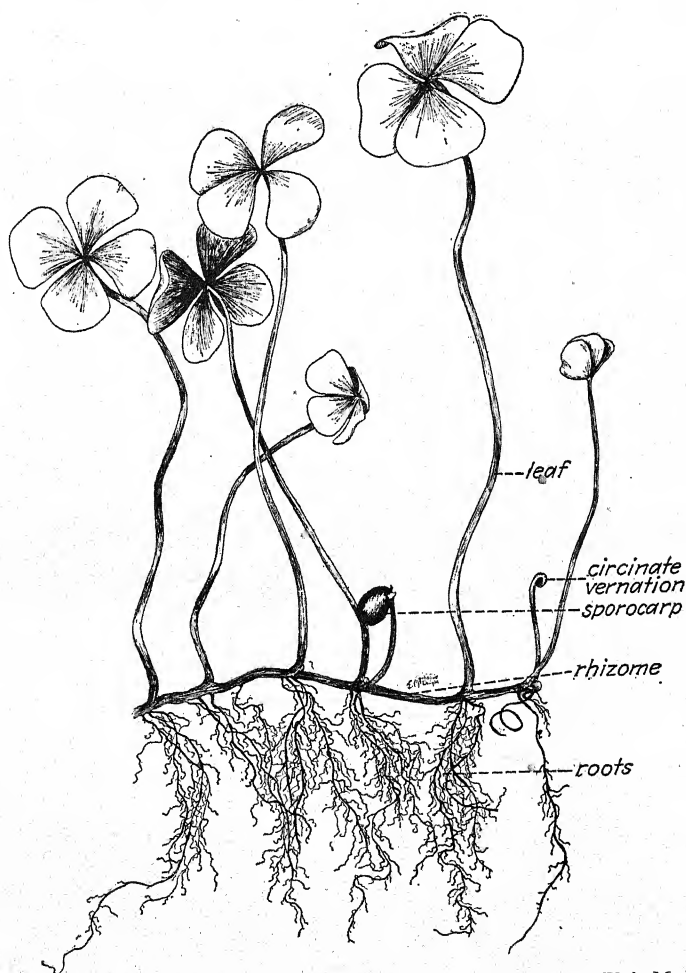


FIG. 243. *Marsilea*, one of the heterosporous "water ferns." (Drawings by Elsie M. McDougale.)

The Structure and Life History of Marsilea. Although there is considerable diversity in the structure and methods of reproduction in the four genera, *Marsilea*, found in widely scattered localities throughout the world, may be taken as a representative of the group. The sporophyte of *Marsilea* has an elongated, prostrate stem which grows above or slightly below the surface of the ground. Roots, growing from the stem or rhizome, penetrate the soil. The leaves of *Marsilea* are four-lobed and very unlike

those of the ordinary ferns; in fact, they greatly resemble four-leaved clovers (Fig. 243). *Pilularia* is very much like *Marsilea*, but its leaves are reduced to mere stalks without an expanded blade. The stem of *Marsilea* is traversed by an amphiphloic siphonostele (Fig. 232). The spores in *Marsilea* are produced on highly modified structures called **sporocarps**, or "spore fruits," which are produced as one or more branches of the leaf petioles. These sporocarps, when mature, are extremely hard bodies.

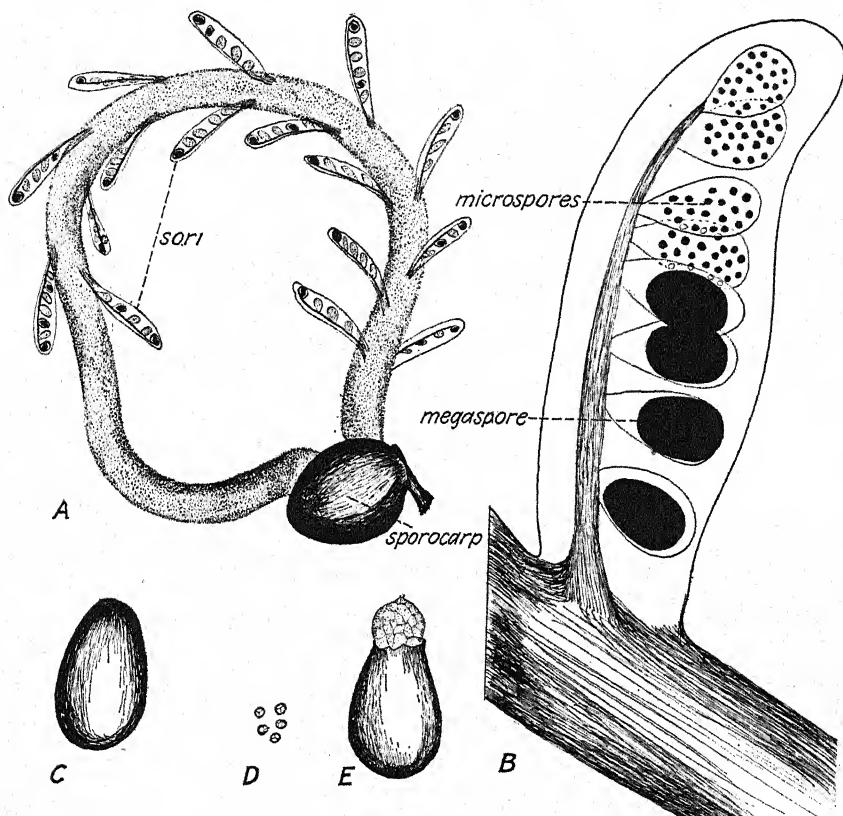


FIG. 244. Sporocarp germination and spores in *Marsilea*. A, sporocarp with protruding gelatinous ring carrying sori; B, a sorus with megaspores and microspores; C, a megaspore; D, microspores; E, a megaspore germinating, with protruding female gametophyte.

Sporangia of two kinds are produced within the sporocarps. One kind of sporangium contains a single large spore called a megaspore (or macrospore), and the other numerous smaller spores called microspores. During their early stages both types of sporangia follow the same course of development each forming 8 or 16 sporocytes and producing 32 to 64 spores. In the microsporangium, all the spores develop, but in the megasporangium, only one of the meiospores develops into a single large megaspore, all others disintegrating. The sporocarp is so hard and so impervious to water that the outer wall must generally be cut in attempts to germinate *Marsilea* artificially. The

sporangia within the sporocarp are attached to a tissue which, upon the addition of water, swells to a remarkable degree. In the process of swelling, this tissue pushes out of the sporocarp as a gelatinous ring, carrying the sporangia along (Fig. 244, A). Within a few hours the sporangia shed the spores.

The spores germinate very quickly after being exposed to moisture. The large spore is packed with starch. Upon germination, it produces a small green thallus which protrudes from one end of the opened spore wall. This is the female thallus (Fig. 244, E). The small spore germinates and produces an even more reduced thallus. It is the male thallus. The spores, therefore, differ not only in size but in function as well. The production of two kinds of spores results in the production of separate male and female gametophytes.

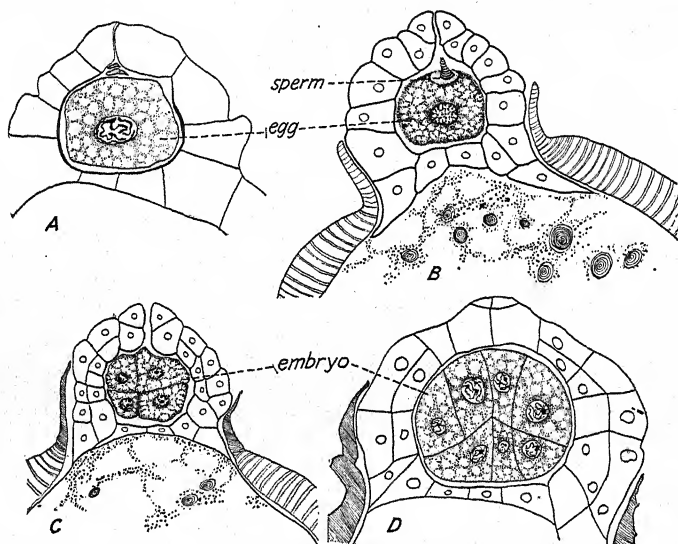


FIG. 245. *Marsilea*. A, detail of female gametophyte, showing archegonium with egg cell and indications of nutritive tissue beneath it; B, fertilization of egg by spirally coiled sperm; C and D, detail of stages in development of embryo still contained in the old female gametophyte; C, four-celled stage; D, number of cells increased by division.

The female gametophyte produces a single, very much reduced archegonium which contains a relatively large egg cell (Fig. 245, A). The male gametophyte, produced entirely within the wall of the microspore, is reduced to a few cells. There is a single cell which corresponds morphologically to the thallus, and the antheridium consists of but a few cells and produces at maturity 32 sperm cells. The sperms are coiled, multiciliate structures and each carries a vesicle which contains some stored food. The sperms swim to the archegonia in water, pass down the short neck, and penetrate the egg (Fig. 245, B).

Fertilization is accomplished promptly by the fusion of the nuclei of the sperm and the egg. The embryo develops rapidly and in the early stages differs in no essential respect from that of the common fern. The young embryo grows attached to the old female gametophyte and spore from which it derives its nutrition (Fig. 245, C, D). It grows rapidly and within a few days has developed roots, stem, and a leaf.

Summary of the Filicales. To the order Filicales belong the common land-inhabiting ferns (the Filicinae), all of which are homosporous, and a very small group of water ferns (the Hydropteridineae), which are heterosporous. The sporophytic phase, characterized by the diploid

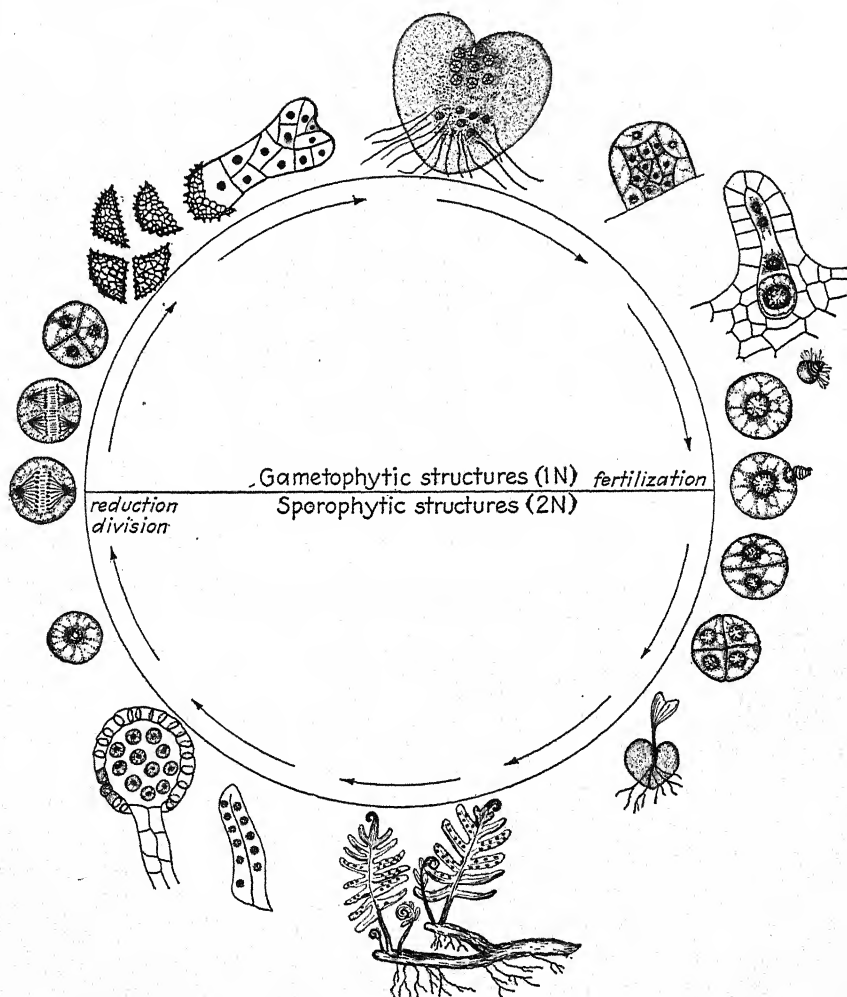


FIG. 246. Diagrammatic representation of the life cycle of a common fern.

number of chromosomes, is the prominent phase of the life cycle (Fig. 246) and the recognized fern plant is a sporophytic rather than a gametophytic structure. This is in contrast to the situation in bryophytes where a gametophytic structure is the recognized plant. The prominent structures

developed during the sporophytic phase of the life cycle are, in the order of their development, the zygote; the embryo with its quadrants forming the foot, root, leaf, and stem; the sporeling, or young sporophyte; and the mature sporophyte consisting of roots, stem, and leaves, the last sometimes differentiated into sterile leaves and fertile leaves, or sporophylls. The sorus with its protecting indusium, the sporangium with all its parts, and the sporogenous tissue consisting of spore mother cells, or sporocytes, are the last structures developed in the sporophytic phase.

The meiotic divisions of the maturation processes occurring in the sporocytes reduce the number of chromosomes from the diploid ($2N$) to the haploid ($1N$). This marks the beginning of the gametophytic phase and the end of the sporophytic phase.

The structures developed during the gametophytic phase, named in the order of their appearance, and characterized by having the haploid number of chromosomes, are as follows: the spores which are the final product of the maturation processes; the thallus (sometimes called the prothallus) which, when full grown, is the mature gametophyte; the sex organs, consisting of the antheridia and archegonia, both borne on the same thallus; and the gametes. The gametes are the last structures produced during the gametophytic phase, and their fusion at fertilization marks the end of the gametophytic phase and the beginning of the sporophytic phase.

ORDER OPHIOGLOSSALES—ADDER'S-TONGUE FERNS

The Ophioglossales form a small order of peculiar and interesting ferns consisting of three genera, two American and one Asiatic. Both of the American genera, *Ophioglossum*, the "adder's-tongue" fern, and *Botrychium*, the "rattlesnake" fern, are widely distributed (Fig. 247). The number of species and of individuals is, however, small.

Sporophytic Structures. The mature sporophytes are relatively small, fleshy, succulent plants that lack the sclerenchyma tissue characteristic of most of the common ferns. *Ophioglossum* particularly is not fern-like in appearance. Their stems are generally small, erect, underground structures that bear a few relatively thick, fleshy roots typically occupied by a mycorrhizal fungus. Often, but not always, a single leaf is produced in a growing season and its development is extremely slow. In *Botrychium* each leaf requires 4 years for development, three of which are spent underground. Leaves of the Ophioglossales typically have a sterile and a fertile portion. The sterile portion becomes well developed and leaf-like. In *Ophioglossum* it has an entire margin and in *Botrychium* it is compound and dissected (Fig. 247). The fertile, or spore-bearing, portion of the *Ophioglossum* leaf is a narrow, somewhat flattened spike; hence the common name "adder's-tongue" fern. Although in some species of *Botrychium* the fertile portion of the leaf resembles that of *Ophioglossum*, usually it is branched, resembling the flower cluster of a grape shortly after pollination. For this reason, *Botrychium* is sometimes called the "grape fern." The leaf parts are compound structures with the sporangia in compact groups from which comes the name "rattlesnake fern," which is sometimes applied to this plant. The third genus of the Ophio-

glossales, *Helminthostachys*, produces leaves with sterile and fertile portions intermediate in form and structure between the two American genera.

In *Ophioglossum*, the sporangia are embedded in the tissue of the fertile spike, but in *Botrychium* the sporangia are more prominent, being superficial on the pinnules of the fertile branch. When the pinnule tissue fails to develop, the sporangia are attached directly to the midrib of the pinnule. The number of spores produced by members of the Ophioglossales is large, ranging from 1,500 in each sporangium of *Botrychium* to 15,000 in some species of *Ophioglossum*. The production of a large number of spores characteristic of many of the early vascular plants is regarded as a primitive feature. Most of the modern ferns, which are thought to be of recent origin, generally produce a small number of spores per sporangium, from 32 to 64 but in rare cases a few hundred.

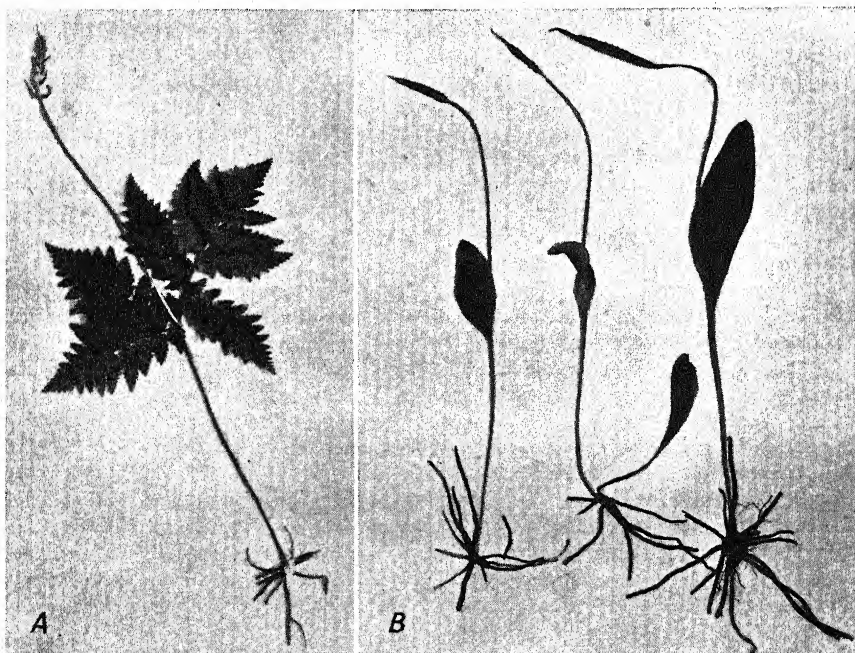


FIG. 247. Ophioglossales. A, *Botrychium* with roots, vegetative leaf, and fertile spike with sporangia; B, *Ophioglossum*, showing fertile leaves, roots, and fertile spikes.

The anatomical features of the stem indicate a high degree of development and an advanced evolutionary position. Although the young plants generally have a primitive protostele, the adult plant stems are usually siphonostelic with collateral bundles that are endarch in most genera. The center of the older stems is occupied by a distinct pith. Surrounding this is a woody cylinder with pith or medullary rays. Outside this is a cylinder of phloem tissue separated from the xylem by a cylinder of cambium. An endodermis surrounds the vascular strand on the outside. These stems with their cambium cylinder are, therefore, capable of some secondary growth, a feature which was common in the vascular plants of past geological ages and is characteristic of the stems of dicotyledons and gymnosperms. Secondary growth is rarely found in living members of the lower vascular plants.

Gametophytic Structures. The gametophytes of the Ophioglossales are peculiarly primitive structures. They are tuberous in form and develop either entirely underground and are without chlorophyll, as in *Botrychium*, or eventually come to the surface and develop green lobes, as in *Ophioglossum*. Rhizoids are present on these gametophytes, but they are not well developed. Characteristically the lower portion of the gametophyte is occupied by an endophytic fungus, while the upper part bears the sex organs, both antheridia and archegonia. The symbiotic association of fungus and gametophyte is regarded as one of the types of mycorrhizal relations already discussed in the chapter on the fungi. Gametophytes showing this association are frequently referred to as "mycorrhizal gametophytes." In this feature and in their tuberous structure, the gametophytes of the Ophioglossales resemble those of the genus *Lycopodium*.

In the Ophioglossales, both types of sex organs, antheridia and archegonia, are borne on the same thallus. The antheridia are large structures that are generally sunken in the tissues of the gametophyte and in general appearance resemble the male gametangia of *Equisetum* and *Lycopodium*. Each antheridium produces a large number of sperms. The sperms themselves are similar to those of the common fern. They are spirally coiled and have many cilia. The archegonium is a short structure with the venter, or enlarged basal portion, sunken in the thallus. The neck of the archegonium protrudes from the surface of the thallus. Structurally, the archegonium of the Ophioglossales is similar to that of the ordinary ferns. There is an egg cell, a ventral canal cell that disintegrates early, and a neck canal cell with two nuclei.

After sperm and egg unite, the zygote divides transversely, forming an upper and a lower segment. Development of the embryo is imperfectly known in many species. In some species, a suspensor is formed, but others lack this primitive feature.

Summary of the Ophioglossales. The members of this order of ferns form a distinct group, showing advanced evolutionary structures combined with primitive features. In the sporophytes, the presence of a cambium cylinder separating the parts of a collateral bundle system in siphonostelic arrangement, and the development of secondary tissues, is evidence of an advanced evolutionary position. Simplicity of form and structure in stem and leaf is regarded as a reduction rather than a primitive feature. The development of tuberous gametophytes is a primitive character, although the form and structure of the sperms are of an advanced nature. The presence of mycorrhizal fungi in the underground tissues of both sporophyte and gametophyte and the lack of chlorophyll in some of the gametophytes are regarded as evidences of degeneration.

THE SPHENOPSIDA—PLANTS WITH WEDGE-SHAPED LEAVES

The Sphenopsida include the extinct order Sphenophyllales, a group of small plants bearing wedge-shaped leaves, several other orders of fossil plants, and the order Equisetales with both fossil forms and the single living genus *Equisetum* to which the "horsetails" belong. Among fossil Sphenopsida were the giant *Calamites*, of the order Calamitales, that lived during the Carboniferous period. These plants were generally slender tree forms, frequently 20 to 40 ft. in height and not usually exceeding 10 to 15 in. in diameter, but sometimes they were larger attaining heights of possibly 100 ft. and diameters of perhaps 24 in. Whatever their size, they had underground rhizomes and jointed, erect, aerial stems, such as those

of the present-day *Equisetum*. Fossil Sphenopsida are found in the Devonian and extend through the Carboniferous and Permian periods of the Paleozoic age. Forms resembling the modern *Equisetum* have been found as fossils in more recent geological periods.

Jointed or articulate stems are characteristic of all Sphenopsida. Both protosteles and siphonosteles are found in the group which is characteristically *without leaf gaps*. The leaves are generally small or reduced but are large in some fossil types. Leaves in the Sphenopsida are usually developed in whorls at the nodes of the aerial stem or its branches. The sporangia are borne on specialized structures or stem appendages, called **sporangiophores**, commonly aggregated into **strobili**, or **cones**.

Classification of the Sphenopsida.¹

Class Equisetinae:

- Order Sphenophyllales..... Fossil forms
- Order Calamitales..... Fossil forms
- Order Equisetales..... Both fossil and living forms

ORDER EQUISETALES—HORSETAILS, OR SCOURING RUSHES

The present-day members of the order Equisetales, comprising about 25 species of the genus *Equisetum*, are but a remnant of a group of plants that, during an earlier geological period, constituted a prominent part of the vegetation of the world. Species of *Equisetum* are commonly called "scouring rushes" or "horsetails." The former designation came from their use in scouring household utensils. The term "horsetail," particularly applicable to the branching forms, is equivalent to *Equisetum*, from *equus*, meaning "horse," and *saeta*, meaning "bristle." Most plants of *Equisetum* now living are of small stature with slender stems less than a yard high; the members of one species, however, are said to have stems 25 to 30 ft. high though not much more than 1 in. in diameter.

Sporophytic Structures. The mature sporophytes are of peculiar form and construction. In some species, they produce aerial stems of two distinct types, one short-lived, unbranched, without chlorophyll, and producing spores in April or early May, the other, sterile, green in color, and persisting through the growing season (Fig. 248). In other species, there is but one type of aerial stem, a green structure bearing a cone at the apex (Fig. 249). Some of the aerial branches are annual, while some persist for more than one year. The stems may have slender branches produced in whorls at the nodes as in *E. arvense*, the common horsetail, or they may be unbranched, erect, and wand-like. All species have an

¹ The reader is referred to pages 328 to 335 for a more extensive and coordinate classification.

extensive development of underground stems, or rhizomes, that are perennial. The vegetative stems are green in color and are the photosynthetic organs. Stems of *Equisetum* are longitudinally grooved or furrowed with ridges alternating with the depressions. In most species, silica is

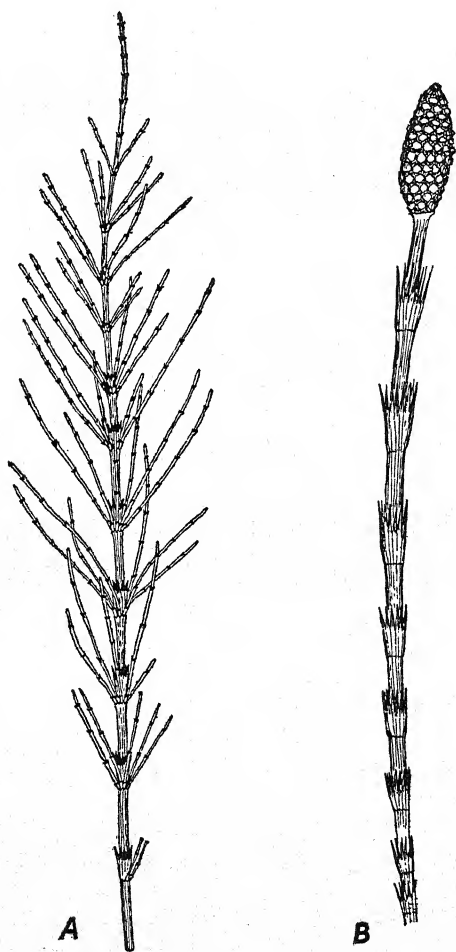


FIG. 248. *Equisetum arvense*. A, sterile vegetative stem; B, fertile stem bearing cone at apex. (Drawings by Edna S. Fox.)

present in the stem. This gives them their value as "scouring rushes." The stems, moreover, are conspicuously jointed and often may easily be pulled apart at the nodes.

In cross section, the stem shows a characteristic structure. The center

is at first occupied by pith, which soon disappears, leaving most of the older stems hollow. The permanent tissues of the stem, epidermis, cortex, and vascular strands form a thin cylinder surrounding the central cavity. Besides the central lacuna, or channel, two other types of longitudinal canals are regularly present in the *Equisetum* stem. These are (1) **vallecular canals** which are located in the cortex, each one associated with a longitudinal groove or furrow of the stem; (2) **carinal canals**, each associated with a vascular bundle, which are located deeper in the tissue on a radius with one of the longitudinal ridges of the stem. The terms vallecular and carinal applied to these canals are descriptive adjectives derived from *vallecula* and *carina*, anatomical designations of groove and ridge, respectively. The vascular system is made up of collateral bundles arranged as a siphonostele. In the internodes, the bundles are distinct and widely spaced with each one located beneath one of the superficial ridges of the stem. In the nodal regions, the bundles form a continuous ring of tissue. Each bundle consists of primary xylem and phloem. While the phloem is well developed, the xylem is sparse and poorly developed (Fig. 265, A). Generally, there is neither cambium nor secondary tissue in the living species of *Equisetum*. Although cambium and secondary tissues are found in the fossil Sphenopsida, these tissues occur in only a few species of *Equisetum* and when present are but feebly developed. Endo-

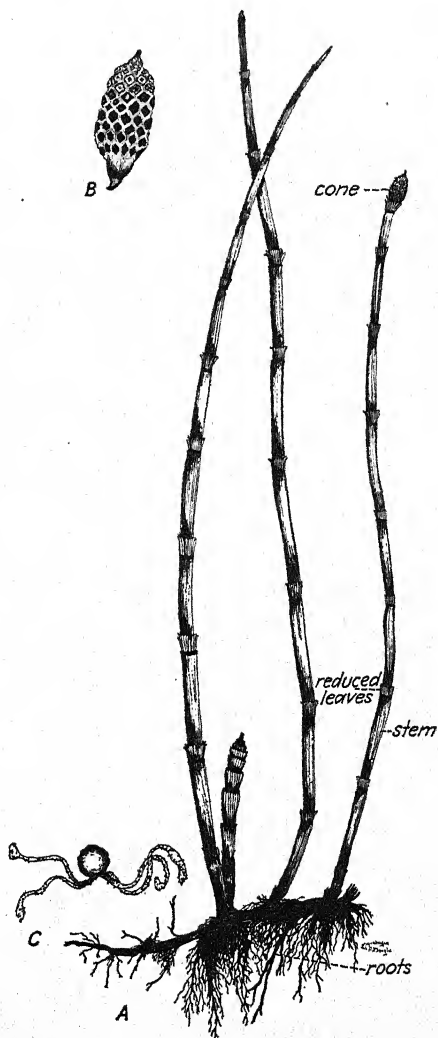


FIG. 249. *Equisetum prealtum*. A, sporophyte; B, detail of cone showing sporophylls; C, one spore with elaters, greatly enlarged. (Drawings by Elsie M. McDougale.)

dermal tissues are regularly present and are well developed in the stems of *Equisetum* and are distributed in a variety of ways. There may be a single endodermis external to the vascular system or there may be both an external and an internal endodermis. In some species, a continuous endodermis is lacking, but in these cases each individual bundle is surrounded by an endodermis. The branches in *Equisetum* arise from adventitious buds developed at the nodes. The leaves are also developed at the nodes and are always reduced scale-like structures that coalesce to form a toothed whorl at each node of the stem. The roots are small and wiry, showing a single vascular strand with the tissues in radial arrangement. Roots are thought to arise from the basal portion of the branch primordia, not directly from the nodal tissues of the main stem. Growth in the sporophyte is by means of triangular apical cells in the tips

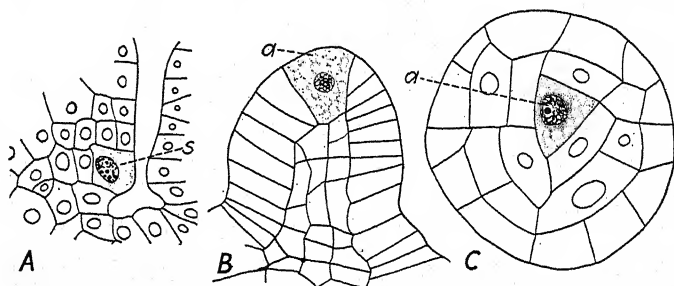


FIG. 250. *Equisetum*. A, sporangium initial, s; B, apical cell, a, in longitudinal section; and C, the same in transverse section.

of the stems, branches, and roots. These apical cells are the primordial meristems and by their division give rise to new cells. The mature tissues of stems and roots develop as the result of growth and differentiation of the segments of the apical cell (Fig. 250, B, C). Apical cells in *Equisetum* are best demonstrated in longitudinal sections of young stem tips of some of the branching forms; they may also be seen in the median sections of the numerous side branches.

The spore-bearing organs of *Equisetum* are aggregated in definite cones at the apex of the stem (Figs. 248, B; 249). The cone consists of a main central axis with specialized spore-bearing structures, called **sporangiophores**, developed in whorls. Each sporangiophore consists of a stalked hexagonal plate bearing several elongated sporangia. These are attached to the cone axis by short stalks at right angles to the stem. The morphological nature of these sporangiophores has been the subject of considerable discussion. By some, they have been regarded as sporophylls, *i.e.*, reduced

spore-bearing leaves. Others believe that all sporophyll tissue has disappeared from the cone and that, in this case, the sporangiophores are specialized structures perhaps more nearly related to stems than to leaves. Whatever the exact morphological interpretation of the sporangiophores, diploid sporocytes in the sporangia undergo meiosis and form quartets of haploid spores that are all alike.

Gametophytic Structures. As in other plants, the spores of *Equisetum* are the product of meiosis and are the first cells of the gametophyte. The four ribbon-like elaters characteristic of these spores are formed from the outer layer of the wall of the spore, *i.e.*, deposited in strips which are broken at maturity. The hygroscopic nature of the elaters results in their curling and uncurling under varying conditions of moisture (Fig. 249, C). Although a few fossil relatives of *Equisetum* were heterosporous, all living plants of this group are homosporous. The spores contain chlorophyll, are dark green in color, and as soon as shed they germinate and produce the gametophytes. The mature gametophytic thallus of *Equisetum* consists of a heavy cushion-like central portion that is several layers of cells in thickness. Green, irregularly shaped lobes grow from the upper surface and marginal regions of the thallus. Rhizoids, attaching the thallus to the soil, are developed on the underside of the central portion of the gametophyte. These gametophytes are definitely dorsiventral, *i.e.*, differentiated into upper and lower sides, and grow in a prostrate position on the surface of the soil. In this growth habit, the gametophytes of *Equisetum* resemble those of the true ferns and differ from those of all other members of the lower Tracheophyta. The cells of the upper portion contain chlorophyll, but those in the lower part are colorless. In earlier accounts, the gametophytes of *Equisetum* were described as showing a tendency to develop separate male and female plants. Later investigations indicate, however, that normal gametophytes grown under natural conditions are monoecious plants that bear both antheridia and archegonia on the same thallus. Apparently gametophytes grown in culture or under crowded conditions may show dioecious tendencies with young plants producing only male sex organs.

The margins of the thalli are meristematic and continue an irregular growth sometimes for as long as 2 years. At maturity, the gametophytes are small, usually less than $\frac{1}{3}$ in. in diameter, although some species are said to produce larger ones that are a conspicuous reddish color. Sex organs, both antheridia and archegonia, develop from superficial cells of the growing tissue of the marginal region. An antheridium of *Equisetum* develops in a manner similar to that of a sporangium of the eusporangiate type. The antheridial initial divides in a plane parallel to the surface of

the thallus, thus forming an outer and an inner cell. Of these, the outer cell develops into the wall of the antheridium and the inner one produces the sperm-bearing tissue. At maturity, the antheridium, containing a large number of sperms, appears sunken beneath the surface of the thallus. In form and structure the antheridium of *Equisetum* resembles those of the marattiaceous ferns and the Ophioglossales, but is unlike the antheridium of the common leptosporangiate fern (Figs. 241, 251). The sperms, produced in large numbers, are large, spirally coiled, motile structures with numerous cilia. The latter feature is characteristic of most of the

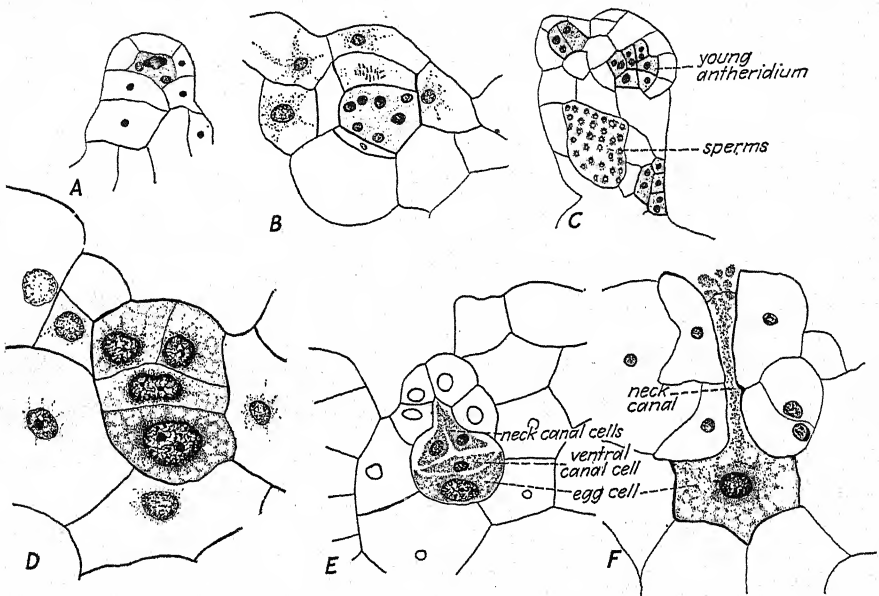


FIG. 251. Structure of sex organs of *Equisetum*. A-C, antheridia; A, young stage; B, intermediate stage; C, young antheridia and older antheridium with sperms; D-F, series of stages in development of archegonia; F, a mature archegonium.

lower groups of the Tracheophyta. The initial cell of the archegonium of *Equisetum* is also a superficial cell of the marginal tissue of the thallus. The archegonial initial divides with a wall parallel to the surface of the thallus much as in the antheridial initial. The outer of the two cells develops the neck cells, and the inner cell forms the axial row of the archegonium (Fig. 251). The axial row consists of the egg, the ventral canal cell, and one or two neck canal cells. The archegonia originate in the general region where the plate-like lobes of the thallus are developing. Growth of the plates leaves the archegonia in the grooves between the

lobes. At maturity, the archegonium is mostly sunken in the thallus, but the end of the neck may protrude slightly (Fig. 251, E, D).

Syngamy and the Development of the Embryo. Several of the motile sperms may penetrate a single archegonium by way of the neck canal, but normally only one unites with the egg, thus marking the beginning of a new sporophytic phase. The development of the embryo is initiated by the enlargement of the zygote and its division in a plane transverse with the long axis of the archegonium. In general, the upper cell of the two thus formed develops into the embryonic stem and leaf. The root is formed from the lower of the two cells. Several eggs may be fertilized, and may develop embryos, in the numerous archegonia on a single thallus. This is an unusual feature in the higher plants.

Summary of the Equisetales. The Equisetales and their fossil relatives represent a highly specialized group of plants that make up one of the great groups of the lower vascular plants. *Equisetum* plants with their slender jointed stems and numerous branches and small leaves, both of which are developed at the nodes, constitute a group that is unique among plants. The stem with its siphonostele and collateral endarch bundles indicates evolutionary advance, but the general lack of cambium and secondary tissues in the living forms shows reduction in these features from the higher development of the early ancestral forms. The spore-bearing organs, the sporangiophores, possibly unrelated to leaf structures, constitute another unique and distinguishing feature. The dorsiventral, prostrate gametophytes with their erect, marginally growing lobes differ from those of all other groups. The gametophytes resemble those of the true ferns in one feature, their habit of growing in a prostrate position on the surface of the soil, in contrast with the radial and subterranean types of many other of the lower vascular plants. They differ from the common ferns, however, in the development of a thick central portion and numerous erect, green, marginal lobes. The sex organs of *Equisetum* are sunken in the thallus tissue, the antheridia developing in the manner of those in the eusporangiate ferns. The sperms are coiled, multiciliate structures.

THE LYCOPSIDA—THE LYCOPODIUM-LIKE PLANTS

The Lycopsidea include both extinct forms, known only from their fossil remains, and living plants. Among plants classified as Lycopsidea there is diversity in size, form, and methods of reproduction, implying a lack of close relationships. The fossil order Lepidodendrales, with its large dendroid types, and the living orders Lycopodiales and Selaginellales are representative of the Lycopsidea. Members of the Lycopsidea line have roots and leaves representing an advance over the Psilopsida. Although

leaves are present, they are usually small and *there are no associated leaf gaps* or breaks in the vascular cylinder of the Lycopsidea. Protosteles, sometimes with radial arrangement and exarch xylem, are characteristic of Lycopsidea, but siphonosteles with central parenchyma have been found in some fossil types and in living members. Sporangia are developed either on the upper or adaxial surface of leaves or sporophylls or in some cases from cells of the stem near the axil of the leaf. Strobili, or cones consisting of a stem or branch axis, and aggregated sporophylls are characteristic of both living and fossil Lycopsidea.

Members of the Lycopsidea were the dominant plants of the coal flora of the Carboniferous period of the Paleozoic Age. The two most important genera of this period were *Lepidodendron* and *Sigillaria*. *Lepidodendron* was an erect dichotomously branched tree; specimens which were 100 ft. in length have been found. Its leaves were linear, or needle-shaped, 6 to 7 in. long, densely and spirally arranged on the stem. The characteristic scars left by these leaves, from which the name *Lepidodendron* was derived (*lepidos*, meaning "scale," and *dendron*, meaning "tree"), may still be seen on the preserved fossils. Unlike the living *Lycopodium*, which they somewhat resembled in form, some of the species of the Lepidodendrales were heterosporous. They were more like the living *Selaginella* in this respect. The *Sigillarias* differed from *Lepidodendron* in general appearance by a usual scarcity of branches, by a shorter more tapering trunk, and by the manner in which the sporophylls were borne. The form of the leaf scar differs from that of *Lepidodendron*. The name *Sigillaria* is derived from the Latin *sigillum*, meaning, "seal," which the leaf scar is thought to resemble. The *Sigillarias* were probably among the largest of the trees of the Carboniferous period, their trunks reaching 6 ft. in diameter. These trunks, like those of *Lepidodendron*, had an unusually thick cork layer. Erect rigid leaves completely covered the young portions of the stem. In contrast to the spiral arrangement of the leaves of *Lepidodendron*, the leaves of some species of *Sigillaria* occurred in vertical rows. The leaf scars on the fossil remains of these trees appear characteristically in parallel lines on the stems.

Besides the large tree forms, there were some much smaller plants, the homosporous *Lycopodites* and the heterosporous *Selaginellites* that lived during the Carboniferous period. These herbaceous fossil forms, resembling the living *Lycopodium* and *Selaginella*, possibly are more closely related to the living forms than are the tree forms *Lepidodendron* and *Sigillaria*.

Classification of the Lycopsidea. For a coordinated classification of the Lycopsidea, the reader is referred to pages 328 to 335. A brief classification follows:

Class Lycopodiinae :

Order Lepidodendrales.....	Fossil forms
Order Lycopodiales.....	Living forms
Order Selaginellales.....	Living forms
Order Isoetales.....	Living forms

ORDER LYCOPODIALES—"CLUB MOSSES"

The order Lycopodiales, like the Equisetales, is rather small; it consists of two living genera, *Lycopodium*, with about 180 species, and *Phylloglossum* with only one species, a native of Australia and New Zealand. The species of *Lycopodium* are widespread throughout the subtropical and temperate zones. The plants are evergreen perennials of relatively small size and in the temperate regions are generally low growing or trailing. In the warmer subtropical regions, many species of *Lycopodium* are epiphytes, growing on trees. Like the Equisetales, these plants represent only a small fraction of the great number of species and individuals that flourished during the Carboniferous period of the earth's history. Because of their form, structure, and low-growing habit, *Lycopodiums* are commonly known in the United States by such names as "ground pine," "trailing pine," "ground hemlock," "club mosses," and, because of their extensive use at the holiday season, as "Christmas greens." A translation of the term *Lycopodium* is "wolf's foot," a common name which is not extensively used. The term "club moss" is somewhat misleading since these sporophytic structures are in no way comparable with true mosses, nor have they any close relationship with the pines and hemlocks, which are seed plants. In parts of Mexico where some species of *Lycopodium* grow as epiphytes on trees, they are commonly called "riscos."

Lycopodium. The various species of the genus *Lycopodium* are familiar plants of mountains and forests (Fig. 252). Much sought after for Christmas wreaths and decorations, they have disappeared from many regions in which they formerly flourished.

Sporophytic Structures. The sporophyte of *Lycopodium* always has a much branched stem that in some species is erect and in others creeping. In the tropics, many of the species are epiphytic on tree trunks. The stem is entirely covered with quite small, elliptical leaves attached by a broad base. In the most primitive species, all of the leaves of the year's growth bear single, rather large sporangia in their axils. In the more advanced species, these sporophylls are smaller in size and lack the green color of the foliage leaves and are closely compacted in an elongated spike or cone (Fig. 307). This differentiation into vegetative leaves and sporophylls is in line with a similar development in the Filicales and is an indication of a high-ranking sporophyte. The sporangia are produced at

the bases of the leaves. Each sporangium originates in a row of several cells occupying a transverse position near the base of the leaf (Fig. 253). At maturity, the sporangium consists of a stalk and a capsule portion. A large mass of sterile tissue occupies the lower central portion of the capsule. This tissue is known as the **subarchesporial pad**. Numerous spore mother cells, or sporocytes, are developed in the sporangium. Upon maturation, each of these produces four spores. Since the spores are all alike in size and function, *Lycopodium* is homosporous.

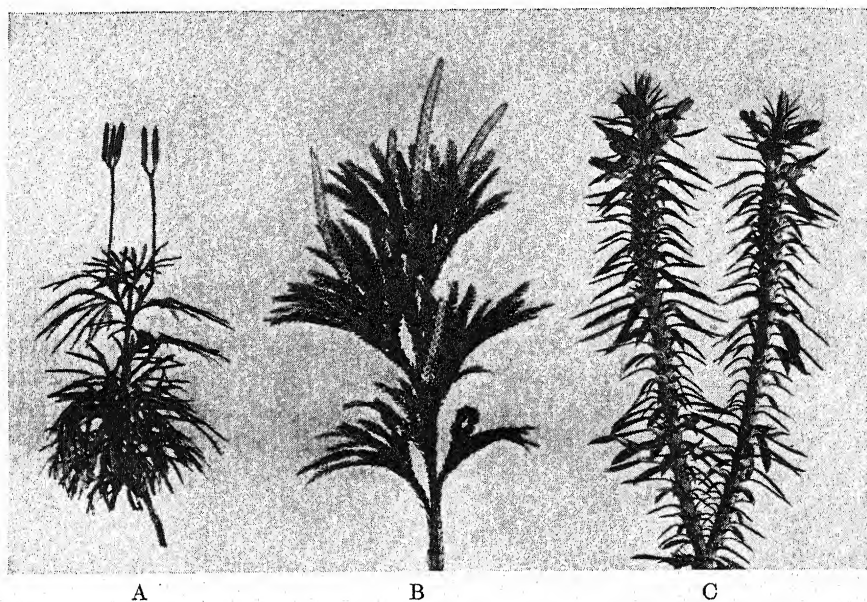


FIG. 252. Sporophytes of three species of *Lycopodium*. A, *L. complanatum*, with sporophylls in stalked cones; leaves scale-like; B, *L. obscurum*, with sessile cones and reduced scale-like leaves; C, *L. lucidulum*, with large bulbils and sporangia in axils of upper leaves. (Photographs A and B by Homer Grove.)

The vascular system of the stem varies somewhat with the age of the plant. In the young stages, it is a radial stele (Fig. 265, C). In some older stems, the stele becomes broken up into isolated bundles with irregular arrangement. Either of these types of steles is of primitive organization, not at all comparable in rank with the siphonostele of the Ophioglossales, previously described. The sporophyte shows a developmental feature of high rank in the presence of an organ developing from one entire half of the fertilized egg and known as the **suspensor**. It is strictly comparable with the suspensor of seed plants, which, it may be recalled, is really not an integral part of the embryo but develops from the zygote in

much the same manner as here (Fig. 112). The only other member of the lower Tracheophyta that develops a suspensor is *Selaginella*.

Gametophytic Structures. The spores of *Lycopodium* are all of equal size; *i.e.*, the plant is homosporous. While the gametophytes of the

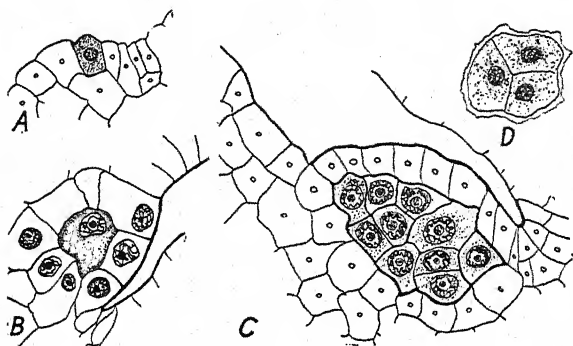


FIG. 253. Stages in development of sporangium of *Lycopodium*. A, sporangium initial; B and C, developing sporangium; D, tetrad of spores.

different species vary considerably in form and structure, those of certain species are, in general, similar to the gametophytes of the Ophioglossales in being cylindrical, tuberous bodies, in some species entirely underground and lacking chlorophyll, and in others partly buried but developing a

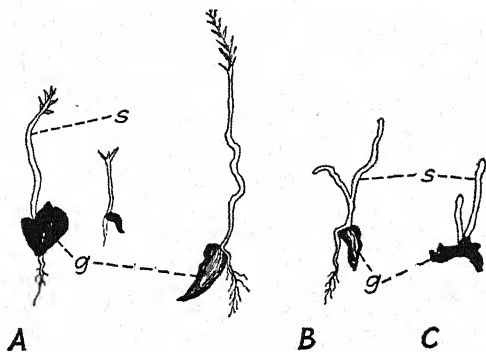


FIG. 254. *Lycopodium* gametophytes, g, with young attached sporophytes, s. A, *L. Selago*; B, *L. complanatum*; C, *L. clavatum*.

crown of green tissue (Fig. 254). Likewise, they have, internally, an endophytic fungus as in the Ophioglossales. The gametophytes of *Lycopodium* are very inconspicuous and are among the most rare of botanical specimens. Until about 1915 they had not been found in America but since that time several collections have been made. These gametophytes

are small, being only a few millimeters in length. Internally there is considerable tissue differentiation in some of them, some showing a central area of elongated cells bounded by two or three zones of surrounding cells that are different in structure and probably to some extent in function. Highly differentiated tissues are not present. Nevertheless, these characters rank the *Lycopodium* gametophyte as a well-developed structure, quite comparable in complexity with those of the thalloid bryophytes and therefore of primitive rank when compared with other gametophytes of the lower Tracheophyta.

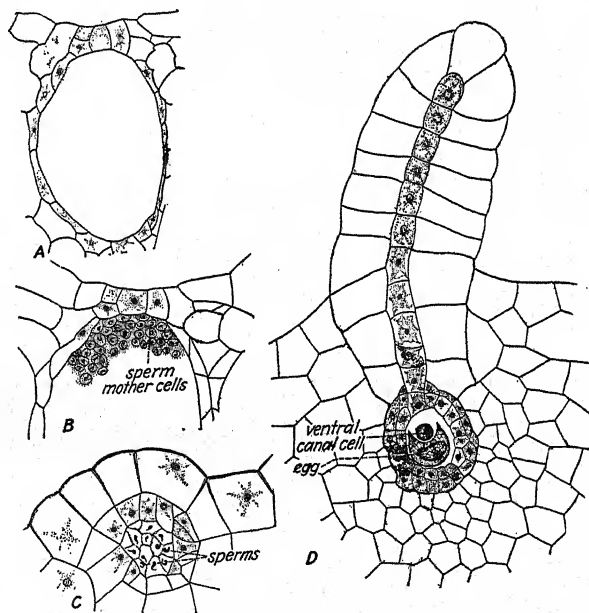


FIG. 255. Details of sex organs of *Lycopodium* sp. A-C, antheridia; D, archegonium.

Antheridia and archegonia are developed on the apex or crown of the gametophyte (Fig. 255). The antheridia develop in the same way as the eusporangium. At maturity, the antheridia of *Lycopodium* are relatively large structures, sunken in the tissues of the thallus, and produce many coiled biciliated sperms, instead of the multiciliated type characteristic of *Equisetum* and the ferns. The archegonia are generally large with long necks of as many as 10 to 14 or more neck canal cells. The gametophytes of some species of *Lycopodium* develop short-necked archegonia with only 1, or a few, neck canal cells. At maturity, the basal portions of the archegonia are sunken in the thallus, but the necks protrude slightly above the surface. A characteristic feature of the gametophytes of *Lyc-*

podium is their slow development after a very delayed germination of the spores. Spores may take 3 years or more for germination.

The Embryo. The embryo of *Lycopodium* develops from the fertilized egg cell, or zygote, in the venter of the archegonium. The first division of the zygote is transverse to the long axis of the archegonium and forms an upper, or outer, and a lower, or inner, cell. The embryo proper is developed from the lower of these two cells while the upper one, called the **suspensor**, remains functionless. The young sporophytes of *Lycopodium*, slowly developing from the embryo, remain attached to the old gametophyte for a considerable time (Fig. 254). Eventually, the gametophyte disintegrates.

Phylloglossum. The genus *Phylloglossum*, usually regarded as a relative of *Lycopodium* and thus another member of the order Lycopodiales, is native to Australia and New Zealand. The plant, combining some primitive and some fairly advanced features, consists of a tuberous stem that bears simple leaves. A strobilus, or cone, of simple sporophylls is produced at the apex of the stem. The plant resembles *Lycopodium* in being homosporous. The gametophytes produced by the spores are of a primitive type, resembling those of certain species of *Lycopodium*. *Phylloglossum*, with an amphiphloic siphonostele, shows a higher anatomical development than *Lycopodium* (Fig. 265, C). Primitive features of *Phylloglossum* are the tuberous stem, homosporous, and tuberous gametophytes. Advanced features are the siphonostelic conditions and the production of a strobilus.

Summary of the Order Lycopodiales. The order Lycopodiales includes two living genera, *Lycopodium* and *Phylloglossum*. The plants are low-growing, herbaceous perennials with terrestrial or epiphytic habit. Anatomically, they are generally of primitive type, *Lycopodium* having a radial stele and *Phylloglossum* an amphiphloic siphonostele. Homosporous characterizes the order, with sporangia borne on sporophylls generally aggregated in cones. The tuberous gametophytes and large sunken sex organs constitute primitive features. The biciliated sperms are characteristic and indicate relationship with the *Selaginellas*.

ORDER SELAGINELLALES—"LITTLE CLUB MOSSES"

The living members of the Selaginellales all belong to a single genus, *Selaginella*, with possibly 600 species.

Selaginella. Numerous species of *Selaginella* occur in the tropics, but only a few extend the range of the genus into the colder temperate regions. The *Selaginellas* are probably related to *Lycopodium*, differing chiefly in being heterosporous.

The Sporophytic Structures. The mature sporophyte of *Selaginella* while somewhat similar to that of *Lycopodium* is usually more delicate (Fig. 256).

The stems are, in many cases, prostrate or only semierect and are sometimes climbing. The vascular system of the stem is usually a protostele though in some species it is a siphonostele or a dictyostele. In the absence of cambium, the bundles are of the closed type (Fig. 265, *D*). Spiral and annular tracheids make up the protoxylem. The metaxylem consists largely of scalariform elements. Of small size and simple structure, the leaves approximate the structure of the leaves of seed plants. They have an epidermis, with stomata mostly on the lower surface of the leaf. Some-

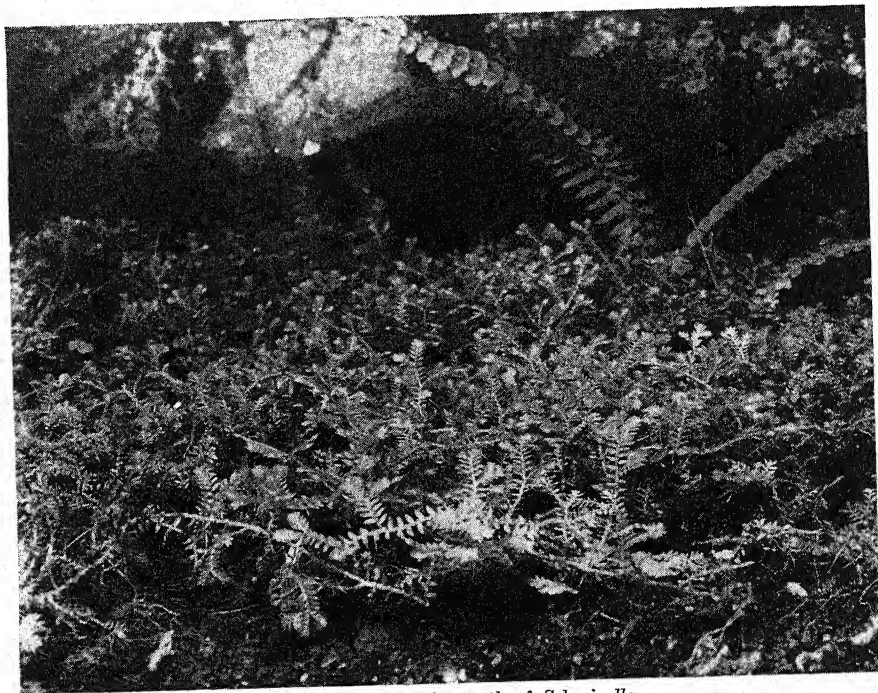


FIG. 256. Habit of growth of *Selaginella*.

times the mesophyll is differentiated into a palisade region and a spongy mesophyll. There is usually a single vascular bundle in the mesophyll. In some species, there are two rows of small leaves on the upper side of the prostrate stem and two rows of larger leaves, one on each of the lateral faces of the stem (Fig. 257). At the base of each leaf is a small membranous outgrowth called a *ligule*, the function of which is in doubt (Fig. 259, *C*). The presence of the ligule can be traced back to paleozoic forms that are thought to be related to and possibly ancestral to *Selaginella*. The ligule helps to differentiate *Selaginella* from *Lycopodium*, which lacks this structure. The roots of *Selaginella* form no extensive system but grow

from unique structures, the **rhizomorphs** or **rhizophores**, that are probably more stem-like than root-like. These rhizophores develop adventitiously on the underside of the prostrate stem and grow downward into the soil or substratum. The roots proper, which are small and fibrous, develop at the tips of the rhizophores. The rhizophore as well as the ligule may be traced through fossil forms to the paleozoic relatives of *Selaginella*.

Growth in the sporophytic structures is by means of apical cells which occupy the tips of the stems and roots (Fig. 259, *D*). The apical cells are the primordial meristem. Growth and differentiation of the segments resulting from the divisions of the apical cell are responsible for the development of the tissues of the root and the stem.

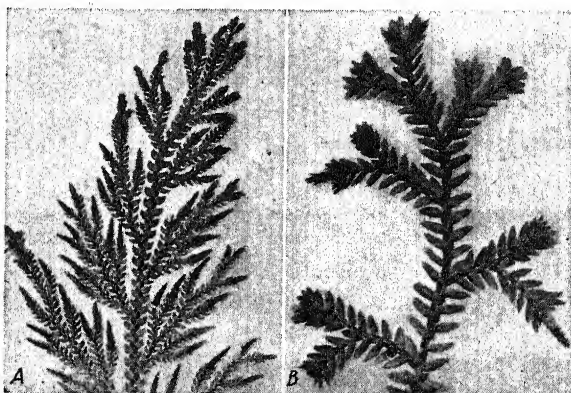


FIG. 257. *Selaginella*. A, *S. Mertensii*, stems, leaves, and cones; B, *S. Krausiana*, stem, leaves, and cones.

a/
not

The sporophylls are grouped in more or less definite cones or strobili at the apices of the branches (Figs. 257, 258). In some species these cones are quite inconspicuous because the sporophylls are not particularly modified in appearance or in arrangement. In other species the sporophylls are smaller and less green in color and are compacted into four-sided cones that are conspicuous, though of small size. These cones produce two kinds of sporangia, microsporangia and megasporangia, producing, respectively, numerous small red spores called microspores and four large yellow spores called megaspores or macrospores. The sporophylls, therefore, may be distinguished as microsporophylls and megasporophylls. Often there is but a single large megasporophyll with a single large megasporangium at the base of the cone, while there are always several or many small microsporangia, one in each of the axils of the upper sporophylls. The sporangia are actually produced from stem tissue in the sporophyll axil and not from the tissue of the leaf. It is more correct to state that the leaves

subtend the sporangia than that the sporangia are borne on the leaves (Fig. 259). There has been considerable discussion concerning the relative

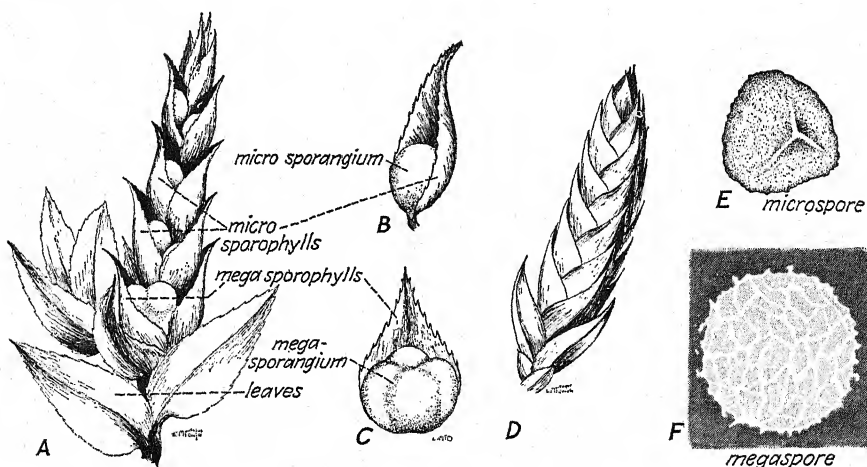


FIG. 258. Strobili, sporangia, and spores of *Selaginella*. A, branch showing vegetative leaves and strobilus with megasporophyll below and microsporophylls above; B, microsporophyll with microsporangium; C, megasporophyll with four-lobed megasporangium; D, strobilus previous to shedding stage; E, microspore and, F, megaspore, both enlarged but not to same scale. (Drawing by Elsie M. McDougale.)

positions of the megasporophylls and the microsporophylls. Some authors state that the megasporophylls are located regularly in the basal or lower portion of the cone and the microsporophylls in the upper

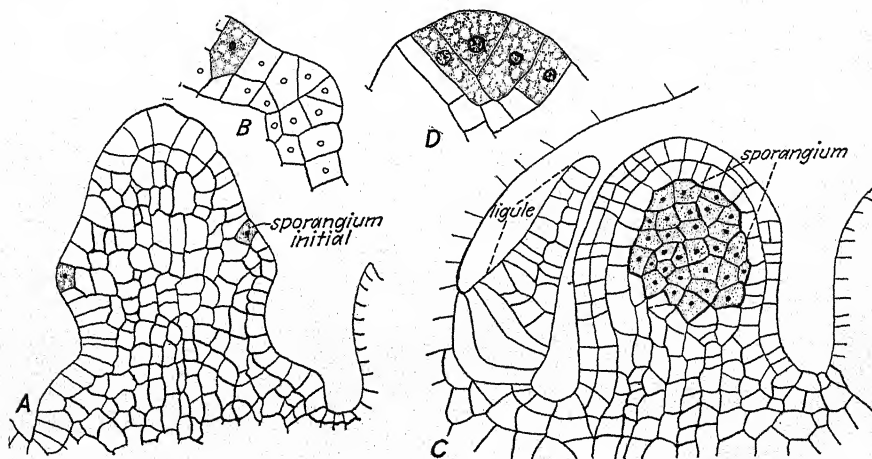


FIG. 259. Structural details of *Selaginella*. A, leaf primordium, with sporangium initial; B, sporangium initial enlarged; C, ligule and young sporangium; D, apical cell.

portion of the cone. However, an investigation of a considerable number of the species of *Selaginella* has shown that no such regularity in position exists. The megasporangia and microsporangia generally occur indiscriminately in the cone.

Early stages of development of microsporangia show that these sporangia are not materially different from those of other lower vascular plants. They contain a large number of microspore mother cells, all of which function in forming quartets of microspores through the usual meiotic divisions, which include a reduction in chromosome number. Therefore, large numbers of microspores are produced in each sporangium.

The development of and within the megasporangium is identical with that of the microsporangium up to the spore mother cell stage, but many of the megaspore mother cells fail to produce spores. In fact, usually but a single one forms a quartet of spores, all the others being used up in the nourishment of this one cell which, therefore, becomes very large, many times larger than a microspore mother cell. Consequently, following the maturation processes, not more than four megaspores are produced in each sporangium and sometimes one or two or three of these may not develop, with the result that often but a single megaspore is produced. More frequently the number is at least two or three, but in these instances the normal reduction division occurs in the spore mother cells.

Gametophytic Structures. It will be recalled that the production of two kinds of spores in heterosporous plants results in the production of separate male and female gametophytes that show conspicuous differences in size and function. In the heterosporous Lycopsidea, the male gametophytes, or microgametophytes, which develop from the microspores are small structures. They lack chlorophyll and are never, to any extent, physiologically independent plants. The female gametophytes, or megagametophytes, are developed from the larger of the two kinds of spores, the megaspores. Although the female gametophytes are also small structures, they are much larger than the male gametophytes. They contain chlorophyll and are to some extent, although not completely, independent plants.

Germination and development of the microspore of *Selaginella* are entirely within the spore wall, which does not rupture until the male gametophyte is mature. In the process of germination, the microspore divides to form a very small vegetative cell and a larger antheridial cell. The single vegetative cell is homologous with the multicellular thalli of the fern and other thallus bodies. The antheridial cell, by a series of divisions, produces a small mass of cells, the outer layer of which becomes differentiated into the wall or jacket of the antheridium, while the internal cells

produce the sperms. Up to this point, the development takes place entirely within the microspore. Microspores are developed in large numbers often in the upper part of the cone. Before the male gametophytes are mature, these microspores, which are red in color, are set free by the bursting of the sporangium wall. The microspores fall out of the microsporangium and some of them lodge near the megasporangium or even within the cleft of the megasporangium wall where they are in the vicinity of the female gametophyte and archegonia. As the sperms mature in the antheridium, within the microspore, the wall of the latter ruptures and the few biciliated sperms produced in each antheridium are set free.

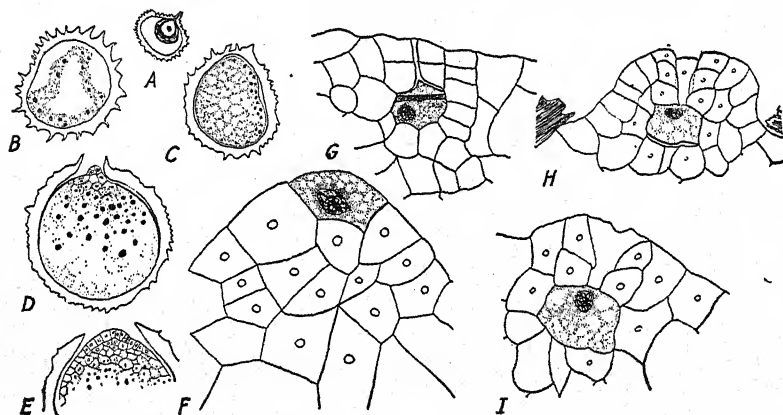


FIG. 260. Stages in development of female gametophyte of *Selaginella*. A, megaspore with single nucleus surrounded by inner wall; B, free nuclei developed by division from A; C, parietal placing of free nuclei; D and E, development of tissue at "beak," enlarged in F to show archegonial initial; G, archegonium with single neck canal cell, ventral canal cell, and egg; H and I, mature archegonium with egg cell.

In the development of the female gametophyte, the nucleus of the megaspore divides many times, forming first a mass of free nuclei that later become surrounded by walls. At an early stage in this development, which takes place at one end of the spore cavity, a large vacuole, said to be filled with an oily reserve food material, appears at the opposite end of the spore (Fig. 260). This eventually becomes filled with cells. Up to this point, the growth of the multicellular female gametophyte takes place entirely within the megaspore wall. Increasing pressure within the spore causes the wall to burst at the apex, where the gametophyte then protrudes slightly. The archegonia are formed in considerable numbers on this protruding portion. The archegonia are very much reduced structures consisting of an egg cell, a ventral canal cell, and one neck canal cell, all of

which are surrounded by a few indefinite wall cells (Fig. 260). Fertilization usually occurs while the megaspores are still within the sporangium.

Fertilization and the Development of the Embryo. When water is available, the sperms freed from the antheridium swim to the archegonium and descend the neck to the egg with which one of them fuses, thus accomplishing fertilization. Union of sperm and egg initiates development of the sporophytic phase, and the embryo begins development immediately. A suspensor is developed as in *Lycopodium*, but it is larger, and its growth, by pushing the embryo downward, aids in bringing the young sporophyte into contact with the storage tissue in the lower part of the gametophyte, where it absorbs nourishment. While an embryonic stem and leaf are formed early,



FIG. 261. Habit of growth of *Isoetes*. (Photographed at Mont Alto, Penn., by Dr. D. A. Kribs.)

the later appearance of the root may be correlated with the large amount of food available in the female gametophyte. Sometime after the embryo begins to develop, the megaspores, with their contained and protruding gametophytes, drop out of the old withering sporangium. At this stage, the embryo plant, with its attached megaspore, or female gametophyte, has the general appearance of a seedling of the seed plants. The roots of the young sporophyte grow into the soil, and the plant begins an independent existence. These structures approach the seed condition very closely. If the megaspore were developed singly in the megasporangium and retained there pending further development of the female gametophyte and, finally, of the embryo following fertilization, the structure would have many of the characteristics of a seed. The consummation of that development may here be anticipated as occurring in the seed plants.

Summary of the Order Selaginellales. Within the single genus of the order *Selaginella* are included about 600 species of mostly tropical, subtropical, and a few temperate zone plants. *Selaginellas* are delicate, herbaceous, perennial plants resembling *Lycopodium*. The anatomical features vary among the species from simple protosteles to siphonosteles and dictyosteles. The presence of ligules and heterospory distinguish *Selaginellas* from *Lycopodium*. Distinct male and female gametophytes of

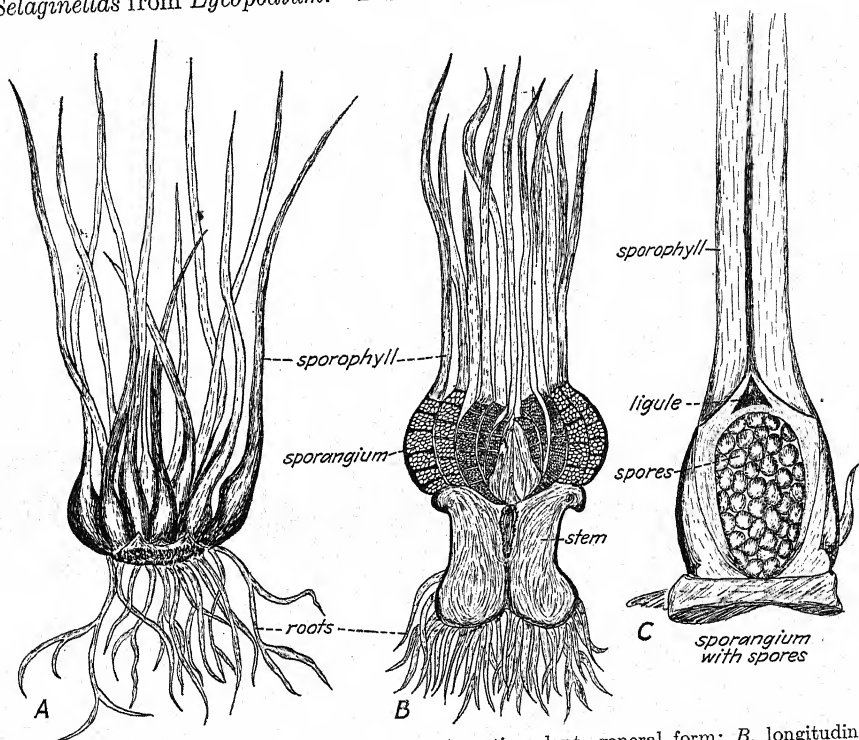


FIG. 262. Leaves and sporangia of *Isoetes*. A, entire plant, general form; B, longitudinal section through plant; C, longitudinal section of one sporophyll with sporangium at the base, showing spores. (Drawings by Clyde Shipman.)

greatly reduced structure differentiate the thalli from those of the members of the Lycopodiales, but biciliated sperms are common to both orders.

ORDER ISOETALES—"QUILLWORTS"

The order Isoetales contains a single living genus, *Isoetes*, with more than 100 species and some extinct fossil forms known as *Isoetites*. In some features the members of this order resemble *Selaginella*. They are heterosporous, ligulate, and their roots are produced on rhizophores similar to those of *Selaginella*. The gametophytes, distinct male and female types, also resemble those of *Selaginella*. The sperms, however, are multiciliated.

Isoetes. The genus *Isoetes* is a native of the north temperate regions, with several species found in the United States. The plants grow attached to the mud in shallow ponds, marshes, and old peat bogs. The plant body consists of a very short stem, producing small, dichotomously branched, fibrous roots and elongated narrow leaves.

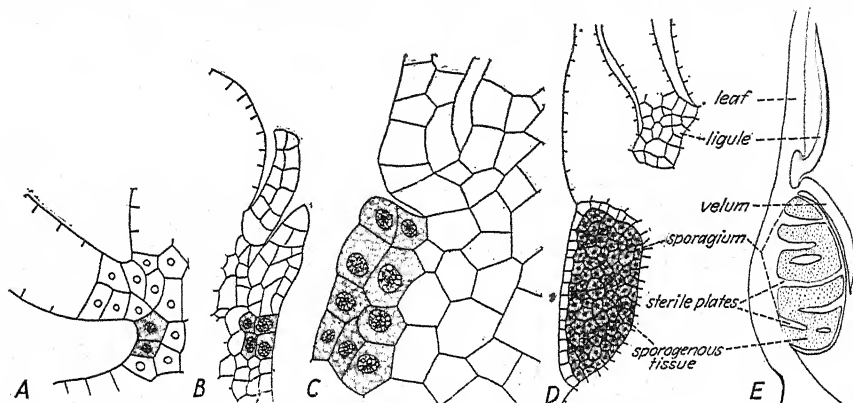


FIG. 263. Sporangium development in *Isoetes*. A, initials of sporangium and ligule; B-D, developing sporangium; E, sporangium showing sterile plates through the sporogenous tissue.

The plants are perennial and range from a few inches to nearly a foot in height. In general appearance, *Isoetes* superficially resembles coarse grass tufts or wild onions (Fig. 261). The leaves are spoon-shaped with enlarged, slightly curved, and overlap-

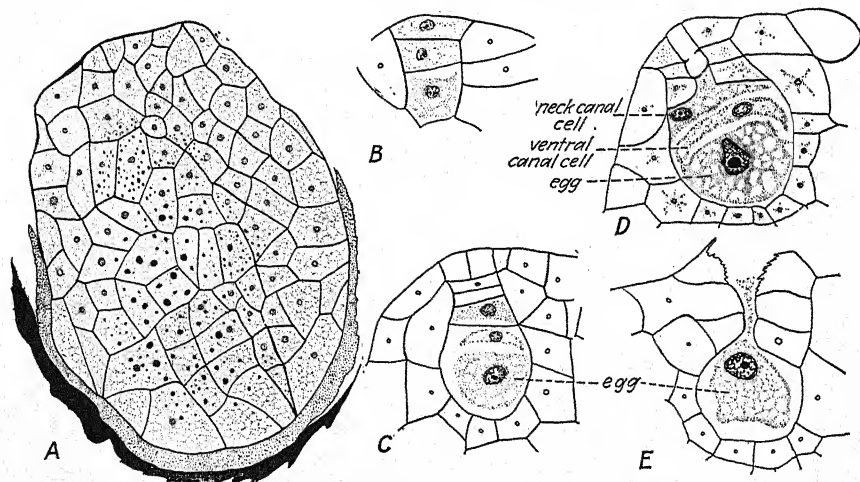


FIG. 264. Development of archegonium of *Isoetes*. A, female gametophyte; B-E, stages in development of archegonium.

ping bases surrounding the short stem and forming a bulb-like structure (Fig. 262). Each leaf is a sporophyll, bearing a single, relatively large sporangium at its base. Ligules, similar to those of *Selaginella*, are located on the leaves just above the sporangia (Figs. 262, 263).

The plant is heterosporous, bearing microsporangia and megasporangia on the same plant. The large sporangia are traversed by plates of sterile tissue (Fig. 263, *E*, *F*). The small bilateral microspores are produced in enormous numbers in microsporangia located on the outer sporophylls. The larger megaspores, though less numerous than the microspores, are abundantly produced in the megasporangia located on the inner sporophylls.

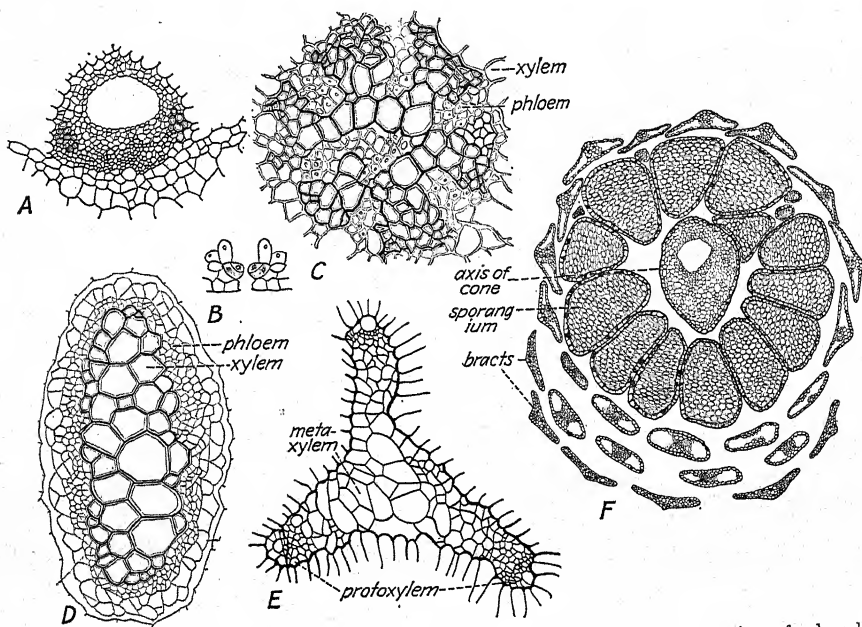


FIG. 265. Anatomical structures in lower vascular plants. A, transverse section of a bundle from the stem of *Equisetum*; cavity in bundle toward center of stem; B, section through stoma from stem of *Equisetum*; C, transverse section through the stem of *Lycopodium*, showing vascular structures; heavy-walled cells are xylem; thin-walled cells between the xylem masses are phloem; this illustrates a radial stele; D, transverse section through vascular strand in stem of *Selaginella*; heavy-walled cells in center are xylem; the smaller, thin-walled cells surrounding the xylem are phloem and parenchyma; this illustrates a protostele; E, transverse section of root of *Sphenophyllum*, an extinct genus related to *Equisetum*; the section shows only the xylem region, protoxylem at the three corners; this is a radial stele; F, transverse section of a cone of *Sphenophyllum Dawsoni*. (F drawn by Paul Sacco.)

Both male and female gametophytes of *Isoetes* are very much reduced structures. Although differing in many structural details, they resemble the gametophytes of *Selaginella* in general features. The archegonia, reduced in sterile tissues, as compared with *Lycopodium*, are much like those of *Selaginella* (Fig. 264). Archegonia are produced on the apex of the female gametophyte, which protrudes from the ruptured megaspore. The male gametophyte, also like that of *Selaginella* and somewhat like that of the heterosporous water fern, *Marsilea*, is produced entirely within the microspore wall. Four multiciliated sperms are produced from each male gametophyte. Multiciliated sperms are not characteristic of members of the Lycopodiales, which typically have biciliated sperms.

THE PSILOPSIDA—THE PSILOTUM-LIKE PLANTS

The Psilopsida, the oldest and most primitive group of vascular plants, include the order Psilotales, represented only by living plants, and the extinct order Psilophytales, found as Silurian and Devonian fossils. In general, the Psilopsida are primitive types of plants without roots and true leaves, although expanded appendages of the stem functioning as photosynthetic organs are present in living forms. Similar structures were apparently present in the Psilophytales. Protosteles are characteristic of the vascular structures, but some living species are siphonostelic in the aerial stems. Leaf gaps, typical of the higher vascular plants, are lacking in the Psilopsida. Sporangia in these primitive plants are borne terminally on the axes of stems and branches or on short lateral stem appendages.

Classification of the Psilopsida. The following is a brief classification of the Psilopsida:

Class Psilophytinae:

- Order Psilophytales... Fossil forms
- Order Psilotales.... Living forms

ORDER PSILOTALES

The order Psilotales has two living genera, *Psilotum*, with only two well-recognized species, and *Tmesipteris*, with a single species. These plants are of special interest because they resemble more closely than any other living forms the extinct paleozoic members of the Psilophytales; the most primitive and oldest vascular plants yet discovered and now regarded as possibly the parent stock from which all other vascular plants may have evolved. The Psilotales are generally considered to be a small living remnant of the Psilophytales, which has continued from the Silurian and Devonian periods to the present without great modification. Because of these facts, studies of the living members of the Psilotales assume importance.

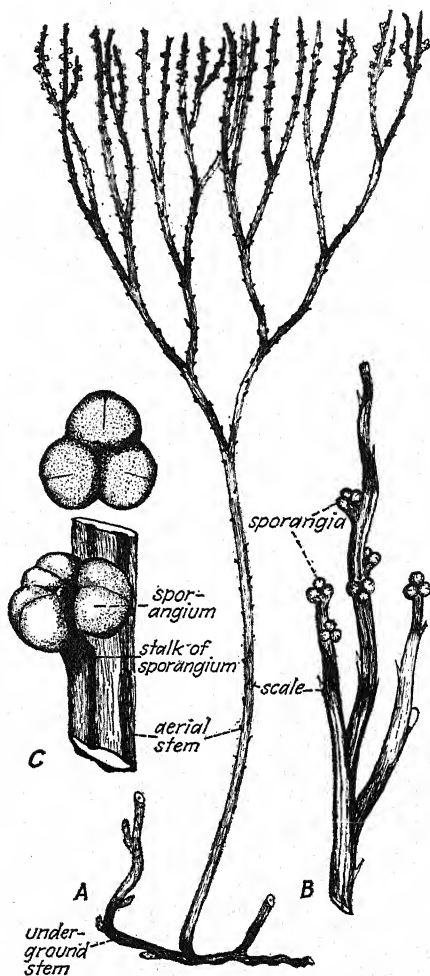


FIG. 266. *Psilotum*, a primitive living vascular plant. A, habit of plant, with rootless, underground stem and aerial, dichotomously branched stem with numerous scale leaves and three-lobed sporangia; B, enlarged portion of branch tips, showing scale leaves and sporangia; C, three-lobed sporangia attached to the stalk; upper figure shows line of dehiscence in each lobe.

Psilotum is native in the tropical and subtropical regions of both the Northern and Southern Hemispheres. It is a small, herbaceous, perennial plant, devoid of roots and true leaves. It grows both as an epiphyte and as a terrestrial plant. The sporophytic plant body consists of an irregularly branching stem, or rhizome, growing underground or in the substratum, taking the place of roots, and erect, aerial, dichotomously branched green shoots (Fig. 266). The aerial stems are ribbed. Anatomically, the stem consists of epidermis, cortex, endodermis, and an exarch star-shaped stele. The radial xylem and phloem surround a central parenchyma region, which in older stems becomes heavy, thick-walled sclerenchyma. The stem of *Psilotum* is regarded as protostelic in the rhizome portion, tending to siphonostelic in the erect parts. The exarch xylem is however more generally associated with the radial protostele than it is with siphonosteles.

The aerial stems of *Psilotum* bear small scale-like appendages alternately on the sides of the stem. In the upper part of the stem, these appendages may form short branches, each bearing a terminal sporangium. The sporangia are generally three-lobed, forming a triangular-shaped structure, each subtended by the sterile branch of the appendage (Fig. 266). *Psilotum* bears but one type of spore and is, therefore, homosporous. Besides reproducing by spores, *Psilotum* multiplies vegetatively by buds, or gemmae, formed on the rhizome, or underground stem. Morphologically, the stem appendages and their fertile parts are regarded as branches of the stem. The fossil Psilophytales support this interpretation by production of sporangia on longer branches of the stem that were, in some cases, definitely terminal on the main axis.

Tmesipteris is found in Australia, New Zealand, and the islands of the Pacific. Generally, it grows epiphytically, but it may be terrestrial. The stem consists of a rhizome and aerial portions, which may be flexuous and pendant. The aerial stems of *Tmesipteris*, like those of *Psilotum*, bear appendages that are, however, larger, more expanded, and green in color. The sporangia of *Tmesipteris* are two-lobed, elongated structures that are borne terminally on short side branches of the stem appendages. This plant is also homosporous.

The gametophytes of the Psilotaes, for a long time relatively unknown, have not yet been studied in complete detail. They are underground structures, cylindrical in shape, of branching form, and inhabited by a mycorrhizal fungus, as are the gametophytes of *Lycopodium* and the Ophioglossales. The gametophytes of both *Psilotum* and *Tmesipteris* are described as resembling the rhizomes of the sporophyte in size and form. Without chlorophyll, they are brown and covered with rhizoids. Sex organs, both antheridia and archegonia, are produced over all surfaces of the same thallus. Antheridia are superficial structures resembling those of the common fern in form and structure. The sperms are multiciliated. Archegonia are developed with the basal portions or venters sunken, but with the short necks protruding from the surface of the thallus tissue. There is evidence that the axial row of the archegonium may be reduced to one or possibly two neck canal cells and a single ventral cell that may function directly as the gamete without the customary division into ventral canal cell and egg.

CHAPTER 18

TRACHEOPHYTA—VASCULAR PLANTS

THE HIGHER GROUPS

Introduction. The designation *higher vascular plants* indicates a group of classes and orders of the Tracheophyta, the members of which produce **seeds**. These plants, formerly included in the spermatophytes, are considered to have attained a higher degree of development than the spore-producing members, or lower vascular plants, discussed in the previous chapter. The seed plants include perhaps as many as 175,000 species. They are the common plants with which everyone is familiar. Geographically, they range from the most northern to the most southern points at which plant life is possible. They occur in water as well as on land, on deserts as well as in humid regions, and on high mountains as well as in lowland regions. In general, they make up the dominant present-day vegetation of the earth. Economically, they overshadow in importance the combined plants of all other divisions. Directly or indirectly most of the food consumed by land animals, including man, comes from them. Man is dependent upon them not only for food but also for clothing, fuel, and shelter. They add very materially to man's aesthetic enjoyment and in many other ways are indispensable to his existence. Structurally, the seed plants are the most complex of all plants. Although there is great diversity in structure and form within the group, its members are alike in the one feature of producing seeds.

The structure known as a seed probably resulted from several features of development which originated in conjunction with heterospory in the lower vascular plants. Outstanding among these was the permanent retention of the megaspore within the megasporangium. The structure from which the seed develops is called the **ovule**, which is a megasporangium enclosed within a covering, or **integument**. The integument later becomes the **seed coat** that encloses the seed with its embryo, or young plant. A seed may be defined as a matured ovule, containing a young sporophytic plant, or embryo, together with stored food.

Comparison of Sporophyte and Gametophyte. As in the ferns and other members of the lower vascular plants and unlike all bryophytes, the sporophyte is the conspicuous structural feature in the life cycle of seed plants. Sporophytes in the higher vascular groups are physiologically independent

plants that vary greatly in size and life span. Some are relatively small plants, while others, like some of the fir, redwood, and cypress trees, are truly gigantic. Many seed plants are annuals, which live but a part of 1 year, while others are perennials living for a number of years. In exceptional cases, trees have persisted through several centuries, and in some cases even for thousands of years, producing new sporophylls, sporangia, and spores each growing season. The gametophytes of seed plants are small, physiologically dependent structures, which live for a relatively short time, some of them but for a few days. The macrogametophytes (female) of some gymnosperms are of macroscopic size. Many others, such as most microgametophytes (male) and the female gametophytes, or "embryo sacs," of the flowering plants, are of microscopic proportions and consist of only a few cells.

Terminology of Reproductive Structures in the Seed Plants. Many of the structures concerned in reproduction in the seed plants were named before much accurate knowledge had been gained concerning their nature, and before it was known that similar structures in some of the lower groups were entirely homologous with them. For this reason, the names commonly applied to the reproductive structures of seed plants are often different from those used for homologous structures in the lower plants. A comparison of the terms used for reproductive structures of the lower vascular plants with the terms used for homologous structures in the seed plants may serve to clarify the situation and lead to a better understanding of the terminology in the discussion which follows.

<i>Reproductive structures of the lower vascular plants</i>	<i>Commonly used terms for the same structures in the seed plants</i>
Megasporophyll.....	Carpel or pistil
Microsporophyll.....	Stamen
Megasporangium.....	Nucellus of the ovule
Microsporangium.....	Pollen sac (part of the anther)
Megaspore.....	Megaspore
Microspore.....	Microspore
Female gametophyte.....	Female gametophyte and embryo sac
Male gametophyte.....	Male gametophyte or germinated pollen grain

Classification of the Higher Vascular Plants. Within the section of the Pteropsida known as the higher vascular plants, two large classes are recognized, the class *Gymnospermae*, or *gymnosperms*, and the class *Angiospermae*, or *angiosperms*. For a classification of these groups, the reader is referred to pages 328 to 335 where these are coordinately listed with other groups. In the *gymnosperms*, the megasporangium is developed on the surface of the megasporophyll, as in preceding heterosporous plants. In this position, usually a single megaspore is matured and produces a fe-

male gametophyte, which develops archegonia and eggs. After fertilization, the tissues surrounding the megasporangium thicken and harden, and internally a miniature sporophyte, the embryo, is developed, the whole structure becoming the **ripened ovule**, or **seed**. In other words, the seed in this group of plants is developed exposed on the surface of the megasporophyll, whence the name gymnosperm, meaning "naked seed." Both the megasporophylls and the microsporophylls are often grouped into **strobili** or **cones**, the former constituting the **ovulate cones**, and the latter the **staminate cones**. Included in this group of plants are the spruces, pines, firs, hemlocks, cedars, junipers, cycads, and related plants.

The **angiosperms** represent an advance in seed development. In this group the megasporangia are not produced on the exposed surface of the sporophylls, as in the gymnosperms, but the outer tissues of the base of the megasporophyll (pistil) entirely enclose the megasporangium, forming a new type of structure known as the **ovary**. The seeds (ovules) thus become enclosed within the ovary wall; from this fact, the name angiosperm, meaning "enclosed seed," has been derived. The megasporophyll (**pistil**), in this group, usually consists of a stigma, a style, and an ovary containing the ovules. The microsporophyll (**stamen**) is made up of a filament or stalk and an anther containing the microsporangia. Both the microsporophylls and the megasporophylls are grouped in the **flower**. The angiosperms are thus the true **flowering plants**. The flowers may contain only microsporophylls or only megasporophylls or both.

Based upon the number of cotyledons, or "seed leaves," that are present on the embryo within the seed, the angiosperms are further subdivided into two groups, the **Monocotyledoneae**, or monocotyledons, having only one cotyledon, and the **Dicotyledoneae**, or dicotyledons, having two cotyledons. Other features of importance in the separation of these two groups are explained later in the text.

THE GYMNOSPERMS

General Features. The gymnosperms are the most primitive of all seed plants and as such extend far back in geological time. In some cases their ages may be computed in millions of years. Certain of the gymnosperms were very much more numerous in past geological ages than they are now. It is possible that these forms were once the predominant flora, as today the angiosperms or flowering plants are the predominant terrestrial plant types. Many species, genera, and even orders of gymnosperms which were abundant in remote geological periods have become extinct and are now known only from their fossil remains. Sections of these fossilized plant tissues are among the most striking of microscopic objects. The detail of cell structure which has been preserved in such fossils is truly

marvelous. In many instances, minute features of the cell walls of plants literally millions of years old have been perfectly preserved in fossil form. A knowledge of fossil plants is essential to a complete conception of the plant kingdom because it is likely that these extinct forms were the ancestors of the present-day plants.

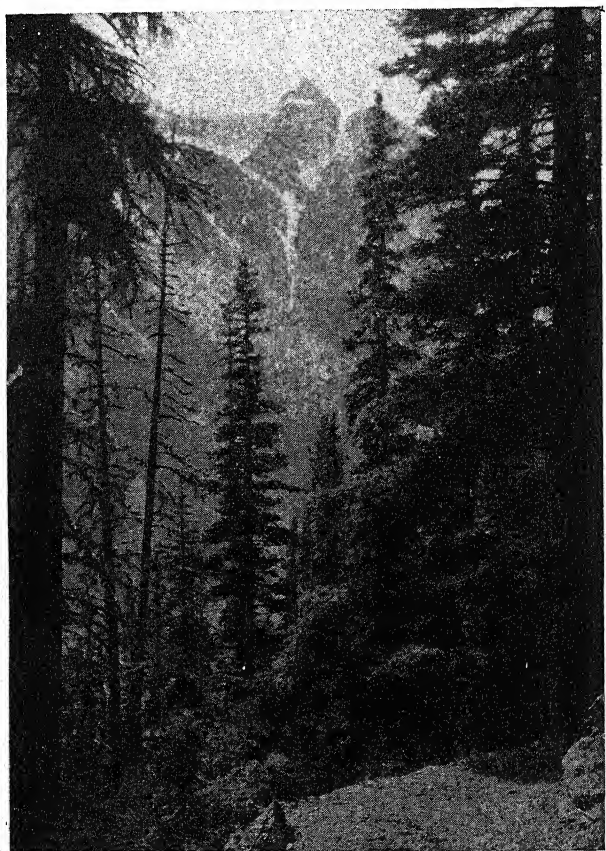


FIG. 267. Coniferous forest near Lake Louise, Canada. (Photograph by Dr. R. S. Kirby.)

While certain kinds of primitive gymnosperms are entirely extinct, other kinds with many primitive features are known both in fossil form and in living forms. These almost extinct groups are frequently represented by only a remnant of a once vast assemblage of species and genera. Among the living forms of gymnosperms are found short, stubby, almost herb-like plants, shrubby and even vine-like forms, and many tree types, some of which, like the cypress and the giant redwoods, are among the tallest trees known (Figs. 268, 269). Descriptions of the forms are given as the special groups are considered.

While certain genera are restricted in their geographical range, the gymnosperms as a group are found throughout the temperate and tropical zones and even in arctic regions. The greatest development of living gymnosperms has been attained by the coniferous forms in the temperate climates of both hemispheres. The once abundant coniferous forests are examples of this development. In general, gymnospermous plants are found in fairly dry situations and in some instances even in semidesert regions.

CLASSIFICATION OF THE GYMNOSPERMS

Class Gymnospermae, or Gymnosperms. Seed plants with ovules and seeds usually borne on the upper side of open scales that are often produced in strobili, or cones. In the case of some primitive forms now extinct, ovules were developed on the surface of or at the tips of unmodified vegetative leaves. Woody tissues are mostly composed of single-celled elements, the tracheids. Two subclasses and seven orders of Gymnospermae are recognized; these are:

Subclass Cycadophytæ. The cycadophyte line.

Order Cycadofilicales or Pteridosperms Fossil forms

Order Bennettitales or Hemicycadales Fossil forms

Order Cycadales Fossil forms and
living plants

Subclass Coniferophytæ. The coniferophyte line.

Order Cordaitales Fossil forms

Order Ginkgoales Fossil forms and
living plants

Order Coniferales Fossil forms and
living plants

Order Gnetales Living plants

Among these orders, two well-defined types of gymnospermous plants may be recognized. These are the **cycadophyte** (the cycad plants) and the **coniferophyte** (the conifer plants) types (Figs. 267, 285). The **cycadophyte** type includes the members of the two fossil orders, the Cycadofilicales and the Bennettitales (often designated fossil cycads), and the true cycads, both fossil and living members, of the order Cycadales. The plants of the cycadophyte type have short, usually thick, unbranched stems, bearing large, fern-like leaves. The stem, in transverse section, shows a large pith, little wood, and a large cortex. *Macrozamia* (Fig. 285) illustrates a large plant of the cycadophyte type.

The **coniferophyte** type includes the members of the fossil order Cordaitales, the order Ginkgoales with its numerous fossil forms, and the single living genus *Ginkgo*, all members, both fossil and living, of the order Coniferales and the members of the order Gnetales, represented by three living

genera. Plants of the coniferophyte type are, in general, plants with tall, slender, branched stems bearing mostly small leaves. The stem, in transverse section, shows a small pith, a large wood region, and a small cortex. Modern conifers, such as the spruce, fir, and pine, are representative of the coniferophyte type (Fig. 267).

Of all the plants of these two types, the members of the order Coniferales form the dominant gymnosperm group of the present. For this reason, they are considered first and in greater detail. The other groups are considered very briefly, later in the text.



FIG. 268. *Juniperus horizontalis*, the dark, low-growing shrub, a conifer growing prostrate on sand dunes and lake shores. (Photograph taken at Lake Bluff, Ill., and furnished by Dr. George D. Fuller.)

ORDER CONIFERALES

General Features. The order Coniferales is represented in the modern flora by 40 living genera and 350 species. They were also represented in past geological ages, as is shown by fossil wood from the rock strata of those periods. In form and size the Coniferales vary from small, creeping, vine-like plants such as *Juniperus horizontalis* (Fig. 268) and shrubby, bush-like plants such as *Taxus canadensis*, one of the yews of the north temperate region, to the "big trees" of California, the *Sequoia* (Fig. 269, B). The majority of the living members of the group are tall evergreen forest trees. Since they are a fairly large group, widely scattered in the

temperate zones of both hemispheres, they exhibit wide variation in most of their features. Not only do they differ in size and form but in structure, leaf form and size, and other characters. Structurally, the conifers are very diverse. Such anatomical features as resin ducts in wood and leaves or parenchyma in the wood show great irregularity in occurrence. Resin ducts are found abundantly in certain genera and are entirely absent in



FIG. 269. A, Douglas fir on Olympic Highway on Olympic Peninsula; B, a specimen of *Sequoia gigantea*, the "General Grant," known as the nation's Christmas tree. (Photographs by Dr. F. W. Owens.)

others. Wood parenchyma may be a conspicuous feature in the xylem of certain genera and very rare in others. Even greater diversity is found in the reproductive structures of the various genera. The gametophytic structures, both male and female, likewise show great diversity, and the embryo, or young sporophyte, varies greatly in methods of development and in structure. The variation in the number of cotyledons of the embryo, ranging from 2 to 15, is an outstanding feature. In the discussion which follows, it is not possible to mention all the variations which occur, but fairly typical structures are considered in the life histories of the group.

Form and Structure of the Sporophyte. As in the lower vascular plants the conspicuous plant body of the conifers is the sporophyte, consisting of roots, stems, and leaves. The members of certain genera of the order are the principal evergreen trees of the north temperate forests. The pine, the spruce, the hemlock, the cedar, and the fir are well-known trees

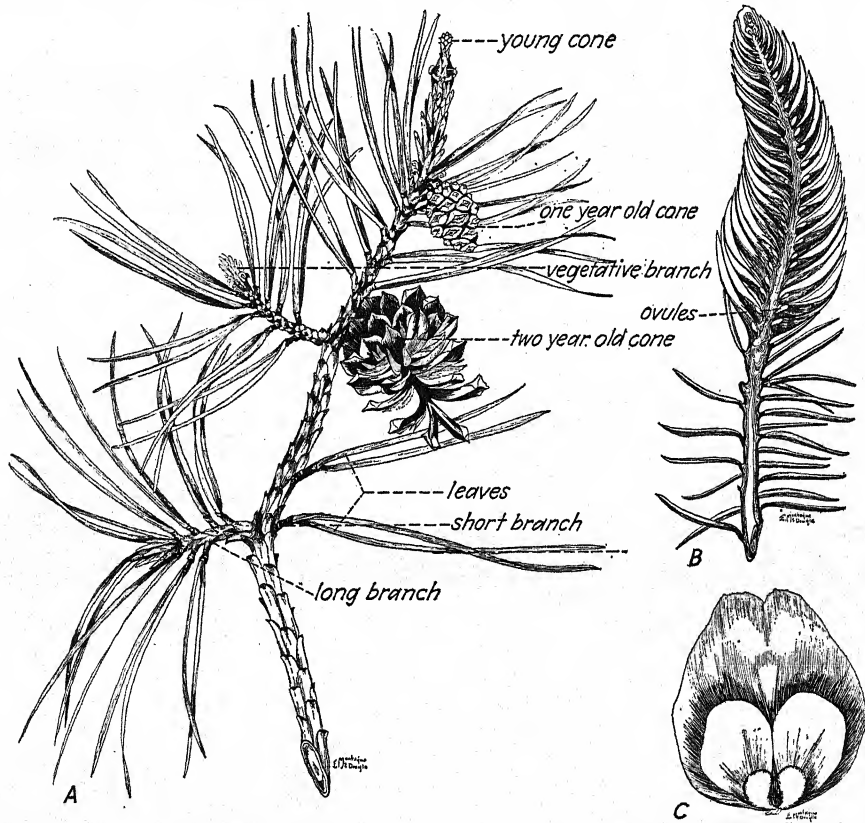


FIG. 270. Leaf, branch, and cone characters of conifers. A, branch of pine with leaves and cones; B, carpellate cone of spruce cut longitudinally to show scales with ovules; C, detail of one scale with two ovules. (Drawings by Elsie M. McDougle.)

belonging to the conifers. In form, nearly all these trees are tall and stately, with straight, excurrent stems. Side branches are characteristically longer on the lower part of the stem, becoming gradually shorter toward the apex. This arrangement of branches gives the tree a graceful tapering appearance. The branches in some genera, such as *Pinus*, to which the pines belong, are of two types, the "long branches," which, when young, bear only nonfunctional, very much reduced "scale" leaves, and the "short branches," which bear the functional needle leaves (Fig. 270).

In the pines the true leaves are produced in clusters. Two to five

leaves are borne attached to a short branch. These short branches develop at intervals on the sides of the longer twigs. Close observation of the very young twig with its fascicles of leaves shows that each of the short-leaf-bearing branches is subtended by a thin scale leaf. The position of the short branch is that of an axillary branch growing from the node on the long branch or twig.

The leaves of the conifers are slender, needle-shaped structures with a heavy epidermis. The group exhibits some variation in the shape and structure of the leaves (Figs. 271, 279, and 280). Some of the genera

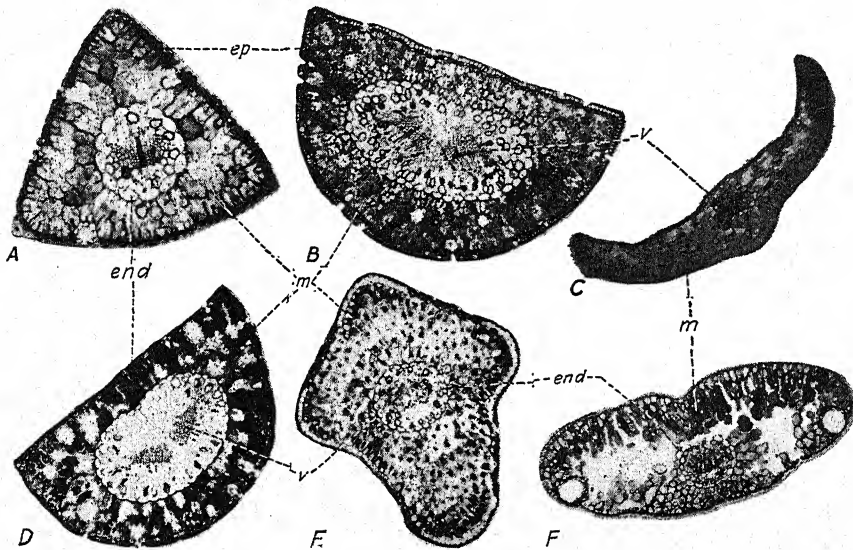


FIG. 271. Photomicrographs of transverse sections of various conifer leaves, showing epidermis, *ep*, endodermis, *end*, mesophyll, *m*, and vascular strands, *v*; A, *Pinus Strobus*; B, *P. laricio*; C, *Taxus* sp.; D, *Pinus* sp.; E, *Picea excelsa*; F, *Pseudotsuga*.

of the conifers have leaves closely appressed to the stem or concurrent, as in the juniper and arborvitae. In size the leaves vary greatly. Most of the trees belonging to this group are evergreen. The leaves are generally retained from 3 to 5 or more years. The needle-like shape and peculiar structure are probably associated with the evergreen habit of the trees. One genus, *Larix*, commonly called the larch or tamarack, sheds its leaves in the autumn of each year and passes the winter with branches bare, as do other deciduous trees.

Anatomically,¹ the conifers show a considerable advance over the living members of the lower vascular plants. The stem of the pine, for example, develops a broad

¹ The anatomical features of the Coniferales are discussed in considerable detail on pp. 176-179. The student is referred to this discussion.

zone of wood or xylem. The phloem is located on the outside of the xylem, with a definite lateral meristem, the cambium cylinder, located between the xylem and the phloem. This cambium layer provides for a continuous increase in diameter. Such increase is accomplished by the division of the cambium cells and the differentiation of the new cells so formed into xylem and phloem. The new xylem cells are added to the outside of the older (primary) xylem cells, and the new phloem cells are added to the inside of the older (primary) phloem. Such growth is termed secondary growth, and the new tissues added are secondary xylem and secondary phloem. In addition to the cambium cylinder, which adds to the xylem and phloem, there is a cork cambium located in the cortical region which continues growth and adds to the general cortical region. Secondary growth in the conifers and in other gymnosperms is a distinct anatomical advance over the lower Tracheophyta, which, in most species, lack cambium and thus are restricted to primary growth.

The phloem of the conifers consists of sieve tubes and phloem parenchyma. No companion cells are present. The sieve tubes have sieve plates located on the side walls. The xylem consists of tracheids and wood parenchyma. Tracheids are single cells functioning as a unit, in contrast to tracheal tubes or vessels, which are characteristic of the angiosperms, and which are made up of many cells joined end to end, forming long tubes. The tracheids of the secondary wood of conifers have bordered pits on the radial and end walls. The tracheids of the primary wood are spirally thickened in the early stages. Later, when growth is less rapid, the tracheids of the primary wood become pitted instead of spirally thickened. Wood rays, consisting usually of single layers of parenchyma cells extending radially through the xylem, are present in most species.

Conspicuous in the tissues of many conifers, and characteristic of these trees, are structures for the secretion and conduction of resinous materials. These structures are called **resin ducts** or **resin canals**. They originate in the parenchyma and are actually little more than large and rather unusual intercellular spaces. Surrounding each of these intercellular spaces is a single layer of thin-walled parenchyma cells, often with conspicuous nuclei and abundant cytoplasm. These cells are the secretory cells that function in the secretion of the resin. The resin is exuded into the canal or duct and is then free to flow slowly through the plant. Generally, the layer of secretory cells is, in turn, surrounded by several parenchyma cells which act as storage tissue.

The Spore-producing Structures—Cones. The sporophylls of the conifers are produced in strobili, or cones, which suggests the name *conifer*, or cone bearer (Fig. 270). Not all conifers produce cones but most members of the pine family regularly do. The cones are of two kinds, the staminate (microsporangiate) and the ovulate (megasporangiate), the latter at maturity being the structures commonly recognized as cones.

The staminate cones consist of a central axis or stem and the attached microsporophylls or scales, each of which normally bears two microsporangia attached to the underside of the sporophyll (Figs. 272, 273, 275). The ovulate cone consists of a central axis and the closely overlapping, attached bracts or scales, some of which are megasporophylls, each normally bearing two ovules attached to the upper side of the sporophyll. These ovules, each of which contains a megasporangium, are

borne freely exposed on the surface of the sporophyll in the manner characteristic of the gymnosperms. Most conifers are monoecious, *i.e.*, bear both kinds of cones on the same tree. Each cone is usually separate from the other kind and generally they occur on separate branches. Ex-

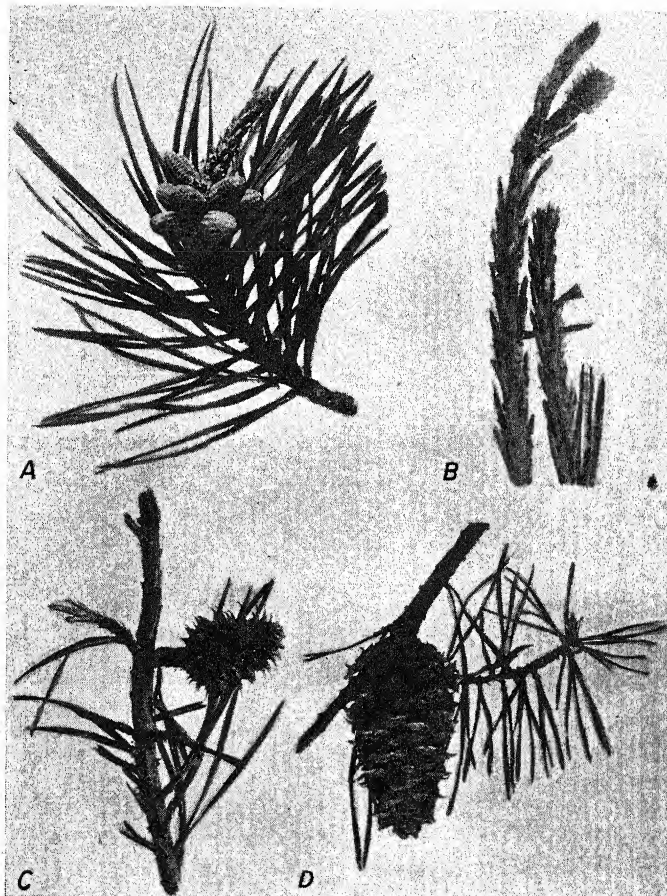


FIG. 272. Cone types in pine. A, a group of mature staminate cones of *Pinus pungens*; B-D, ovulate cones of *P. virginiana*; B, young, C, one year old, and, D, ready to discharge seed. The ovulate cones of pine reach maturity after two seasons' growth.

ceptions to this condition are found. The plants of some species are prevailing dioecious, *i.e.*, bear only one type of cone on a tree. Rarely, on monoecious plants, cones occur which are bisporangiate, *i.e.*, bear both megasporangia and microsporangia on different parts of the same cone.

The staminate cones are small, rather inconspicuous structures, enduring in most genera but a few weeks in the spring season. The exact

length of time during which the male cones persist varies in the different genera. The male cone bears the microsporophylls. Each microsporophyll, in most of the common genera, bears two microsporangia on its underside. Within the microsporangium, the microspore mother cells (microsporocytes) are produced. These, by the processes of maturation (Fig. 276), involving meiosis, give rise to the microspores, or **pollen grains**. Each microspore mother cell forms a spherical tetrad of four microspores. These microspores are produced in tremendous numbers and appear at maturity as a yellow dust or powder. The microspores have the haploid ($1N$) number of chromosomes and initiate the male gametophytic phase.

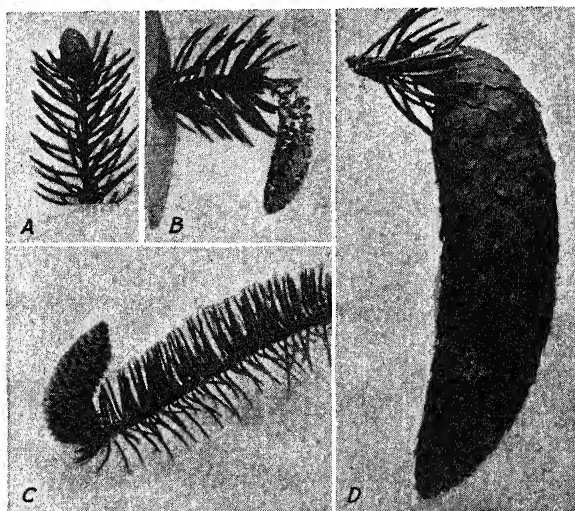


FIG. 273. Cone types of spruce, *Picea excelsa*. A, young staminate cone; B, mature staminate cone; C, ovulate cone at time of pollination; D, mature ovulate cone. The ovulate cones of the spruce reach maturity in one season.

The ovulate cones are of longer duration than the staminate cones (Figs. 270, 274). In some genera, the ovulate cones develop in 1 year, as in the spruce (Fig. 273); in others, as in the pine, 2 years are required for development. After maturity, the cones may remain on the trees, in some cases, for several years after shedding their seeds. In the early stages, the ovulate cones of most genera are very inconspicuous, so much so that they may entirely escape observation. There is considerable discussion as to the exact structure of the ovulate cones in the pines. These cones are comprised of groups of paired structures attached to the axis. The lower one, a short sterile bract, may perhaps be homologous with a leaf. The upper one commonly called an **ovuliferous scale**, or ovule-bearing scale, may perhaps be regarded as a reduced branch. These

two types of scales or bracts are readily observed in the cones of most genera. They are joined together at their bases, the ovuliferous scale being the uppermost. The ovules are located on the upper surface of the ovuliferous scale. It should be recalled at this point that the ovule consists of the megasporangium, surrounded by a special covering, called the integument, which later becomes the seed coat. In the pines, the megasporangium is an ovate body and the integument covers it as a cup-like overgrowth. At the tip of the ovule the encircling parts of the integument do not quite come together, leaving an opening called the *micropyle* (little gate). This opening allows the pollen grains to enter and come into contact with the megasporangium.

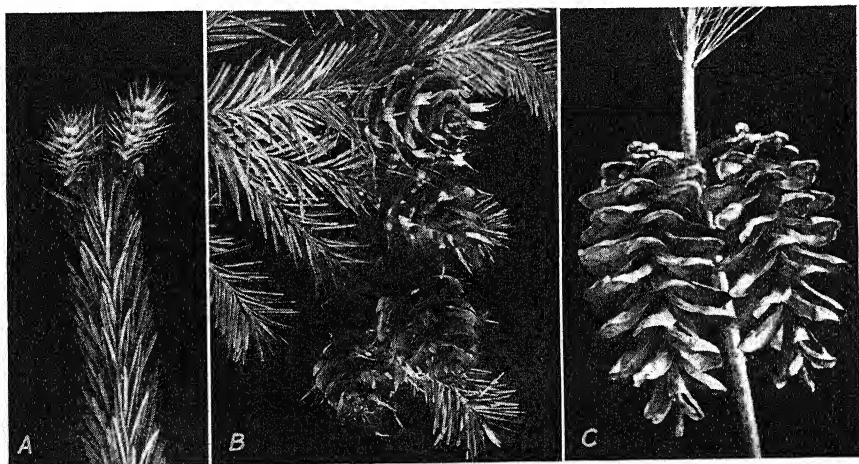


FIG. 274. Cone types of conifers. A and B, ovulate cones of *Pseudotsuga taxifolia*, A, young, and, B, mature (one year old); C, mature ovulate cone of *Pinus Strobus* (two years old).

The megasporangium, now called the **nucellus**, is the inner tissue of the young ovule (Fig. 275). This tissue is generally undifferentiated in the young stages, but, sooner or later, one or several megaspore mother cells appear toward the center of the nucellus. Though in most of the common genera but a single spore mother cell is formed, in some genera, and under certain conditions, from one to five or six may be formed. Each megaspore mother cell, by the regular maturation processes, including meiotic division, gives rise to a group, or quartet, of four megaspores, each with the haploid ($1N$) number of chromosomes. Recent investigations, however, indicate that in pine only three cells are formed. The four cells of the tetrad are usually arranged in a vertical row in the sporangium, forming what is called a **linear quartet**. The linear arrangement of the megaspores is characteristic of nearly all of the seed plants, but it is not

universal. In the arbovitae (*Thuja*), the spores are a tetrahedral rather than a linear group. Not all the members of the quartet develop into functional megaspores; generally but a single functional megaspore is formed. In some genera, however, where the number of spore mother cells is larger, there are several functional megaspores. It is to be noted that, contrary to the condition found in the production of microspores, the megaspores are never shed but are permanently retained within the megasporangium. On germination, the megaspores give rise to the female gametophytes, which likewise are retained within the megasporangium.

Since the members of the Coniferales are perennial plants, it cannot be said that the maturation processes end the sporophytic phase, as can be

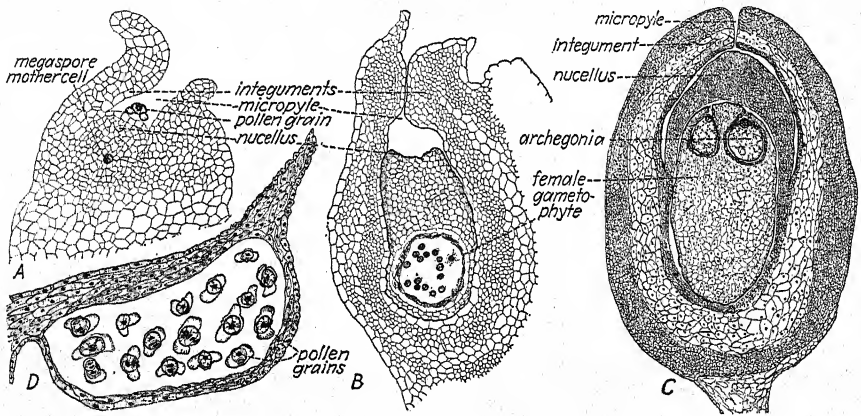


FIG. 275. Development of the reproductive structures in the Coniferales. A-C, longitudinal sections through ovules; A, young stage with pollen grain shortly after pollination; B, free nucleate condition of the female gametophyte; C, older stage with mature female gametophyte showing two archegonia; D, section through microsporangium of staminate cone of spruce showing the mature pollen grains. (A and B drawn by Helen D. Hill; C and D by Jeannette Ritter.)

truly said in reference to these events in some of the lower plants. It may be said, though, that the maturation processes initiate the gametophytic phase, resulting in the development of the male and female gametophytic structures, the surrounding sporophytic structures (leaves, roots, and stems) persisting from year to year and developing a new succession of gametophytic structures each season.

The Gametophytic Structures. Heterospory, found in the lower vascular plants as an occasional situation, is established as the universal condition in the gymnosperms. The tendency, first observed in the lower vascular plants, of the reduction of the gametophytic structures, is carried much further in the gymnosperms. Both male and female gametophytes show very marked reduction in their structures. In the male gameto-

phyte of the Coniferales, the sperms are reduced to nonmotile cells, a feature here found for the first time in the evolution of plants. It should be noted, however, that swimming sperms still occur in two orders of the gymnosperms, the Cycadales and the Ginkgoales. This lack of motility

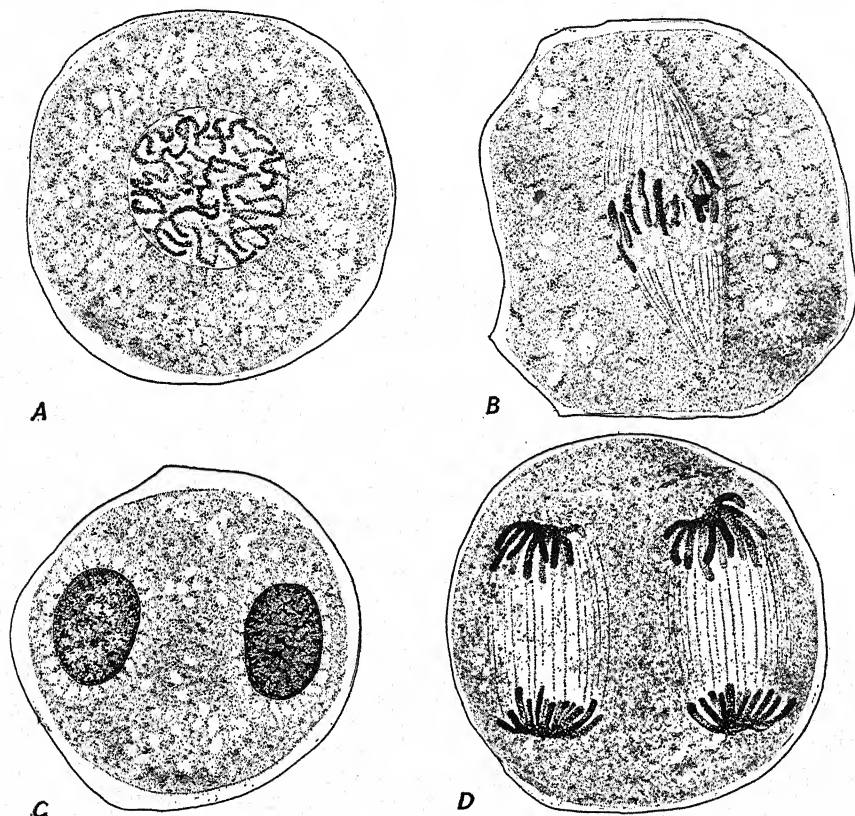


FIG. 276. Maturation divisions in microspore mother cells of conifers; A, prophase; B, metaphase of first division; C, diad stage; D, anaphase of second division. As a result of these divisions, four microspores are formed in each microspore mother cell as shown in Fig. 277, A.

in the Coniferales is just another step in the reduction of the gametophytic structures.

The development of the female gametophyte takes place entirely within the megasporangium, or nucellus, of the ovule (Fig. 275). The gametophyte is entirely dependent for nutrition upon the old sporophytic structures. In the pine, usually only the basal megaspore of the linear tetrad develops into a female gametophyte. In certain other genera, more than one female gametophyte may develop in each ovule.

An account of the development of the female gametophyte of pine by

W. H. Emig is at variance with the previously accepted descriptions. Emig's studies, extending over a period of several years, indicate that the functional megaspore remains in a resting condition for a time and begins to develop only after a considerable portion of the nucellus tissue (sporangium) has been digested by the surrounding nutritive, tapetal-like tissue. The megaspore then, occupying a central position in a vacuole resulting from the digestion, undergoes a series of divisions, which results in the production of about two thousand nuclei. These nuclei occupy a central position in a common mass of cytoplasm and later become separated by walls, the formation of which begins at the micropylar end and eventually extends to the base of the gametophyte.

Emig explains the common interpretation of the parietal location of the nuclei as based on views of aborting ovules, which are common in the pines. According to his interpretation, the growth of the young gametophyte is actually centrifugal, from the center toward the outside, and never centripetal. Finally, the entire female gametophyte becomes a solid ovate mass of tissue.

Archegonia are generally developed at the micropylar end of the ovate female gametophyte (Fig. 275, C). Each archegonium develops from a single superficial initial cell of the gametophyte and consists of a very short neck, a ventral canal cell, and an egg. There are no neck canal cells, the neck consisting of only the wall cells, which vary in number from 2 to 8, or 12, with 8 the most common number. The ventral canal cell is usually a smaller cell than the egg cell, soon disintegrating and leaving the egg cell the sole content of the archegonium. The wall of the archegonium is made up of the adjacent sterile vegetative cells of the female gametophyte, called the "archegonial jacket," which, in addition to serving as the archegonium wall, seem also to act as nourishing cells for the archegonium.

At maturity, the archegonium is an oval structure rather deeply sunken in the female gametophyte. The neck of the archegonium is overgrown by the adjacent cells of the female gametophyte. The contents of the archegonium consist of the egg, with nucleus and abundant cytoplasm, which fills the entire structure. Generally, all the archegonia are grouped in the same region of the female gametophyte. The archegonia in the conifers vary greatly in number in the different genera. In some, as in the pine, from two to five archegonia are developed, while in others, as in the giant redwood (*Sequoia*), the number is reported to be sometimes as high as 60. Other genera have archegonia varying in number from 2 to 100.

The early stages of the male gametophyte (Fig. 277) occur entirely within the microspore wall. As it develops further, the structure may be called a pollen grain. Eventually the pollen tube grows out from the pollen

grain. In the pine, the first divisions within the microspore result in the production generally of two sterile **vegetative cells** (Fig. 277, *B*). These are small lens-shaped cells usually occupying one side of the developing pollen grain and disintegrating very soon. They are regarded as vestiges of the gametophytic thallus commonly developed in the lower groups.

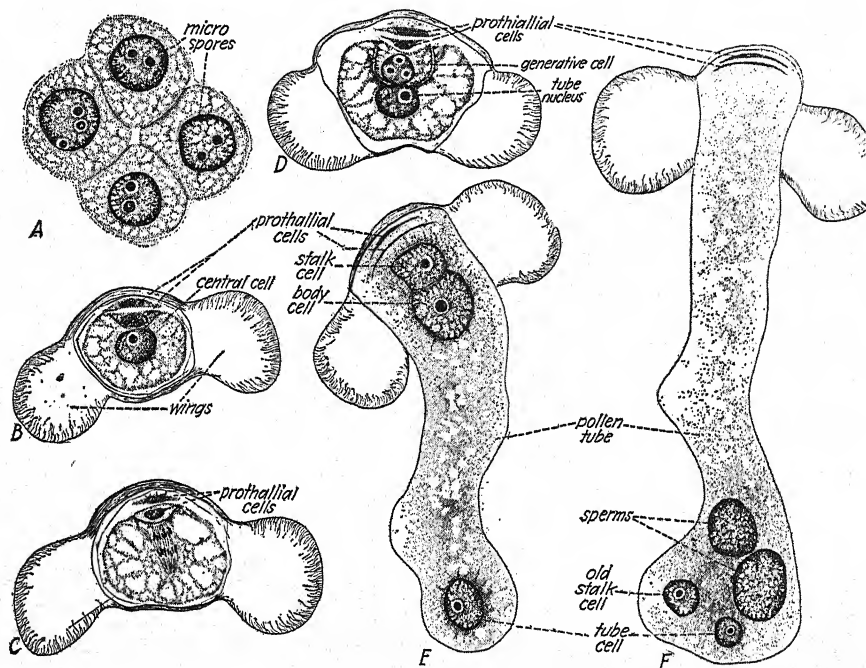


FIG. 277. Microspores and development of the male gametophyte. *A*, tetrad of microspores resulting from divisions shown in Fig. 276; *B*, pollen grain with two prothallial or vegetative cells, central cell, and wings; *C*, division of central cell to form generative cell and tube cell; *D*, stage showing generative cell, tube cell, and two prothallial cells; *E*, diagrammatic representation of germinating pollen grain, showing the development of the pollen tube; the two prothallial cells are shown degenerated; the generative cell has divided to form a stalk cell and a body cell; *F*, diagrammatic representation of mature pollen tube with contents; the body cell has divided to form the two male cells or sperms; the stalk cell, the tube cell, and the prothallial cells are still visible. (Drawings by Helen D. Hill.)

In other genera related to the pine, the number of vegetative cells may vary from none at all to as many as 48. Where they occur, they are formed by successive divisions of the central cell of the microspore.

Following the formation of the vegetative thallus cells, the central cell comes to be the **antheridial cell**, being considered homologous with the antheridium of the lower plants. This central cell, or antheridial cell, divides, forming two cells, the **tube cell** and the **generative cell**. The function of the tube cell is to produce the **pollen tube**, which may be regarded

as a gamete carrier in this group. The generative cell is a small spherical cell which consists of a large nucleus, a relatively small amount of rather dense cytoplasm surrounded by a delimiting membrane, but no cellulose wall. The generative cell floats free in the cytoplasm of the tube cell. The function of the generative cell is eventually to produce the **sperms**, or **male gametes**. Typically in the pine, the young male gametophyte, or content of the pollen grain, now consists of four cells, the two sterile vegetative cells, the tube cell, and the generative cell (Fig. 277, *D*). At about this stage of development, the pollen grains are shed from the microsporophylls and are transported to the female cones where they come into contact with the ovules (Fig. 275, *A*). The pollen of some genera is winged, while in other genera it is wingless. When present, the "wings" are formed by the extension or inflation of the outer covering of the spores. These extensions occur on two sides of the spore, forming a pollen grain with two wings.

Pollination is the term applied to the transporting of the pollen grains from the microsporangia to the megasporangia. In the conifers, this is usually accompanied by the floating of the pollen grains through the air from the male cones to the female cones; this is called wind-pollination. The young female cones at this time stand erect at the ends of the twigs. The pollen grains, when they reach the female cones, fall down among their scales, reaching the ovules and megasporangia at the base of the scales or megasporophylls. From the integuments, the ovules secrete a drop of resinous material into which the pollen grains fall. Eventually, this resinous material dries and pulls the pollen grains through the micropyle, bringing them into contact with the tissues of the megasporangium or nucellus. Pollination occurs early in the development of the female cone. Following pollination, the male and female gametophytes complete their development.

After a period varying in length in the different genera, the pollen tube begins to grow, penetrating the tissues of the megasporangium. Early in the period of pollen-tube growth, the tube nucleus migrates from the pollen grain to the tip of the pollen tube. Later, the generative cell divides into two cells, one termed the **stalk**, or **wall cell**, and the other the **body cell** (Fig. 277, *E*). The stalk, or wall cell, is sterile and does nothing further. It is thought possibly to be a remnant representing the wall, or stalk, of the antheridium. As the pollen tube elongates, the stalk cell passes down into the tip of the tube. The final division which occurs in the male gametophyte is the division of the body cell to form the two **male gametes** (Fig. 277, *F*). The male gametes in the Coniferales are without cilia and thus nonmotile and are carried by the pollen tube to the neck of the archegonium. The designation of the male cells as sperms is

in accord with their origin and function and seems justified, even though they are without motility. The male gametophyte is entirely dependent upon the nutrition derived from the sporophytic tissues of the nucellus or megasporangium, upon which it develops as a sort of parasitic body.

Fertilization. When the two gametophytes, the male and the female, are mature and have produced their gametes, conditions are proper for fertilization. The pollen tube with its two male cells, or sperms, grows for a considerable time through the tissue of the megasporangium which surrounds the female gametophyte. The cells of the megasporangium, or the nucellus, develop a cone-shaped mass between the micropyle and the female gametophyte. Through this cone-shaped mass grow the pollen tubes, generally several in number, and eventually reach the female gametophyte. Here a pollen tube grows into the neck of an archegonium, crushing the neck cells, and penetrates the archegonium. With this development, the final divisions in the pollen tube and in the archegonium occur, forming the two sperms from the body cell in the pollen tube, and the egg and ventral canal cell within the archegonium. These last gametophytic divisions constitute the final acts in the formation of gametes and occur just before fertilization. There are then four cells in the pollen tube, the tube cell, the sterile wall cell, and the two sperms. When the pollen tube penetrates the archegonium, its contents are discharged.

Actual fertilization is accomplished by the fusion of the nucleus of the sperm with the nucleus of the egg (Fig. 278, A). This results in the doubling of the number of chromosomes. Only one of the sperms fuses with the egg, the second sperm, together with the tube nucleus and the wall cell, disintegrating. Reports of fertilization indicate that sometimes only the sperm nucleus fuses with the egg nucleus, the cytoplasm being left behind in the cytoplasm of the egg, but that in other instances the whole sperm cell, nucleus and cytoplasm, fuses with the egg nucleus. In either case, fusion is accomplished slowly, with the chromosomes of each gamete remaining distinct for some time. In the pine, the haploid ($1N$) number of chromosomes has been reported as 12 and the diploid ($2N$) as 24. With the fusion of the nuclei of the two gametes, the gametophytic phase ends, and a new sporophytic generation is originated.

The time elapsing between pollination and fertilization varies considerably. In some genera, pollination and fertilization occur during the same summer. This is true of the spruce, hemlock, arborvitae, and others. In such genera the time between pollination and fertilization is a matter of a few weeks. In other genera, including the pine, pollination occurs in the spring of one year and fertilization in the spring of the year following, a period of about 11 months. The time is related to the rate of growth of the gametophytes, the genera in the first category having rapidly growing

gametophytes and those in the second having slowly developing gametophytes.

The Embryo, the Seed, and the Seedling. As previously mentioned, the embryo of the Coniferales differs considerably in the various genera. The development of the embryo in the pine, being well known, is considered in this discussion (Fig. 278).

After fertilization, the nucleus of the zygote divides. The two resulting nuclei also divide, thus forming four nuclei which migrate to the base

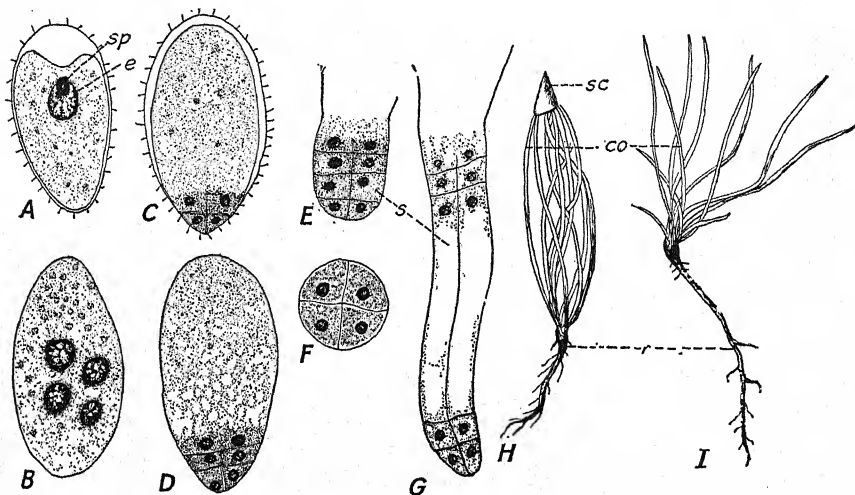


FIG. 278. Fertilization and development of the embryo in conifers. *A*, fertilization accomplished by the fusion of the sperm nucleus, *sp*, with the egg nucleus, *e*, initiating the development of the embryo; *B*, early development of the embryo; *C*, the four nuclei shown in *B* settle to the bottom of the archegonium and each divides, resulting in two tiers of four cells each; *D* and *E*, continued development of the embryo, forming additional tiers of cells; *F*, cross-sectional view of *E*; *G*, formation of suspensor cells, *s*, by the elongation of the third tier of cells from the top; the tip cells eventually form the embryo proper; *H*, germinating seedling with root, *r*, cotyledons, *co*, and old seed coat, *sc*; *I*, slightly older seedling with branched root and cotyledons. (Drawings by Helen D. Hill.)

of the egg and arrange themselves in a plane. A simultaneous division of the four nuclei results in the production of two tiers, each consisting of four nuclei. Following this, walls begin to develop, separating these nuclei. The outer tier of nuclei do not have complete walls, but the cells are open on the upper side and the nuclei are therefore connected with the general cytoplasm of the original egg. Divisions in the upper and lower tiers follow, and, as a result, the embryo consists of four tiers of four cells each.

The lowest of these four tiers of cells becomes the embryo proper, actually forming the young pine plant. The tier adjacent to it forms the suspensor, an elongated structure which pushes the developing embryo deep into the

old female gametophyte, which is rich in stored food. By cell division, cell growth, and differentiation, the complete embryo is eventually formed. The embryo in the pine is polycotyledonous, but certain other conifers are dicotyledonous.

The seed in the conifers is a rather complicated structure. It consists of an embryo protected by a thick and usually very hard seed coat. The embryo, or young sporophytic plant, is surrounded by a mass of stored food, which is the old female gametophyte tissue. The seed coats and other surrounding tissues are derived from the nucellus, or old megasporangium, and the integuments of the ovule.

There is considerable variation of size in the seeds of conifers. Certain species of pine in the southwestern portion of the United States bear seeds which are large enough to be used as human food. These are the piñon pines. The piñon nuts, as these seeds are called, are eaten by the residents of these regions much as peanuts are in other portions of the country.

The seeds generally germinate slowly after a prolonged resting period. Some, however, are reported to germinate before the seeds are shed from the cone. Upon germination, the embryo emerges, usually pushing the seed coat up through the ground ahead of the cotyledons. Finally, the several cotyledons are freed from the seed coat and the young seedling conifer begins a long period of growth to develop a mature sporophyte (Fig. 278, *H, I*).

Summary of the Life History in the Coniferales. In the Coniferales, as in all gymnosperms, the sporophytic phase is of long duration and during this period of the life history a relatively large sporophyte is produced which generally attains the proportions of a tree. During its lifetime, the sporophyte produces many generations of spores. The spores are of two kinds, microspores and megaspores. The sporophyte, as usual, is characterized by having the diploid number of chromosomes in its nuclei. During the maturation processes at the meiotic division, in the formation of the microspores and the megaspores, the number of chromosomes is reduced from the diploid ($2N$) to the haploid ($1N$) number. The spores which are produced as a result of the maturation processes contain the haploid number of chromosomes. All the structures produced from the spores have the haploid number of chromosomes and are, therefore, gametophytic.

The gametophytes are of two kinds. The male gametophytes are produced from the microspores which are formed in the microsporangia and the female gametophytes from the megaspores which are formed in the ovules. The megaspores and the resulting female gametophytes are permanently retained within the ovules. The male gametophytes are much reduced in size, consisting of only a few cells within the original cell wall

and finally the pollen tube and male gametes. The female gametophytes are small oval masses of tissue produced by the megaspores. This tissue is held within the old megasporangium, or nucellus, within the ovule. Generally, several much reduced archegonia, containing female gametes or eggs, are produced at the upper end of the female gametophyte. There is

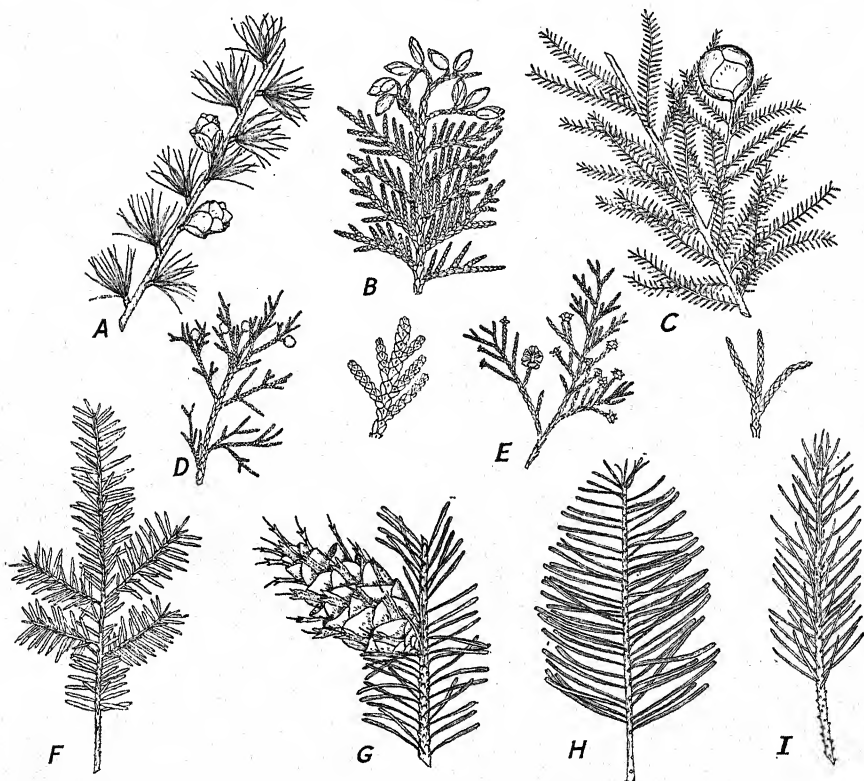


FIG. 279. Leaf and cone characters of some of the better known conifers. A, *Larix americana*; B, *Thuja occidentalis*; C, *Taxodium distichum*; D, *Juniperus scopulorum*, with detail at right; E, *Chamaecyparis lawsoniana*, with detail at right; F, *Tsuga*; G, *Pseudotsuga*; H, *Abies nobilis*; I, *Picea*. (Drawings by Edna S. Foz.)

considerable variation in the different genera in the length of time it takes for the gametophytes to reach maturity and produce gametes. In the pines, generally about 12 to 14 months elapse between pollination and fertilization. The union of the gametes doubles the number of chromosomes to the diploid number and starts the new sporophyte. Embryo, seedling, and finally a mature sporophyte in the form of a tree, all characterized by the diploid number of chromosomes, complete the life cycle.

Common Genera and Species of Conifers. There are about 40 genera, with approximately 350 species in the order Coniferales. These are divided into two families,

the Pinaceae, consisting of 29 genera and 245 species, and the Taxaceae, consisting of 11 genera and 105 species. The members of the family Pinaceae are characterized by the production of distinct ovulate cones with overlapping sporophylls protecting the ovules. The seeds ripen dry. To this family belong the following genera: *Pinus*, the pine; *Larix*, the larch; *Tsuga*, hemlock; *Pseudotsuga*, the Douglas fir; *Abies*, fir; *Sequoia*, redwoods; *Taxodium*, the bald cypress; *Juniperus*, the common cedar; *Thuja*, the arborvitae (Fig. 279); *Araucaria*, a Southern Hemisphere conifer; and *Agathis*, a broad-leaved tropical form (Fig. 280, F).

The family Taxaceae is characterized by the absence of distinct ovulate cones (Fig. 280). The solitary ovules are exposed, and the seeds develop a fleshy covering, or *arile*. The most prominent genera of this family are *Podocarpus*, a native of the Southern Hemisphere, and *Taxus*, the yew, of the Northern Hemisphere.

Both families are represented in the flora of North America, but the family Pinaceae includes all but two (*Taxus* and *Torreya*) of the 14 genera native to the region north of Mexico. The great interest and sentiment that have always been associated with the cone-bearing trees, their wide distribution, and great economic importance may justify a more extended presentation of the characteristics of native American genera.

The genus *Pinus* includes all of the true pines (Figs. 270, 272, 274, C). They are to be recognized by their long needle-like leaves produced in clusters of two, three, four, or five. A single species, the nut pine, of limited distribution in the Far West and the Southwest, produces its leaves singly, as do all other conifers except the pines and larches. Each cluster of leaves is surrounded at the base by a thin, dry membranous sheath. All species are evergreens, the needles remaining on the trees for from 2 to 10 years. In the different species the needles vary from only 1 to 12 or 15 in. in length, the greatest lengths being attained by the "longleaf" pine of the Southern states. Resin ducts are present in the leaves. The cones are frequently produced in clusters and in some species remain on the tree for many years after the seeds are shed. The seeds do not usually mature until the summer of the second year following their formation. In many species the cones are very spiny at maturity. No other conifers have spiny cones. Economically, pines are the most important of all northern timber trees, with the possible exception of the oaks. They yield lumber of the highest quality for construction work, although as a group their lumber is not durable in contact with the ground or in damp situations. Commercially, pine lumber is of two types, the harder yellow-pine type and the softer white-pine type. At present, the best yellow-pine lumber comes from the Southern states and includes such trees as the shortleaf, the longleaf, and the loblolly pine. White-pine lumber is obtained from the eastern white pine, western white pine, sugar pine, and others. Western yellow pine or bull pine is often sold commercially as white pine, which it resembles in texture. Pines are frequently used as ornamental trees and a number of foreign species have been imported for this trade. Pitch, turpentine, tar, and resin are other commercial products of the pines. Thirty-four species of pines are native to the United States.

The genus *Picea* includes all of the true spruces (Fig. 273). All species are evergreen, with straight tapering trunks. The needles are short and often stiff, usually four-angled as seen in cross section, and do not contain resin ducts. They are attached to all sides of the stem and, when they fall, they leave on the stem a short, rather sharp base or cushion. The cones are matured in one season and are pendulous on the branches. Usually they are produced only at the very apex of the tree. Commercially, spruces are important timber trees in the Northern states and in Canada. As pulpwood for paper making, they are unsurpassed. As ornamental trees, they probably surpass in value all other conifers. The blue spruce, with beautiful blue-green foliage, is in great demand for planting. Seven species are native to North America.

The genus *Abies* includes the firs, which are likely to be confused with spruces but are distinguished by the flattened and usually softer needles that leave only a slight circular scar where they fall from the branches. As in the spruces, the needles are produced singly. They are short, contain resin ducts, and come out from all sides of the stems, though appearing in many species to be produced only from two opposite sides. The cones stand erect on the branches at the apex of the tree and mature their seeds in one season. The trunks of firs are straight, tapering, and unbranched, and the bark of small trees contains conspicuous blisters filled with a liquid resin which is used commercially in medicine and is known as balsam. Commercially, they are important timber trees and are used to a considerable extent for ornamental plantings. On this continent, the seven species range only through the Northern states and Canada.

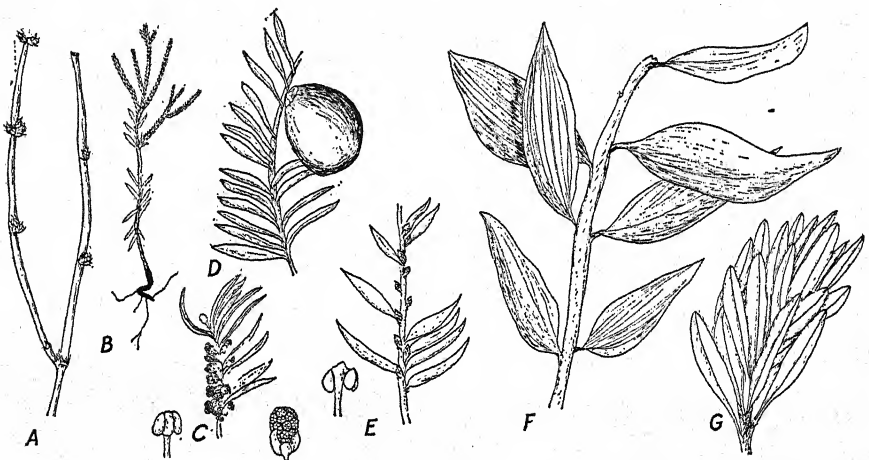


FIG. 280. Leaf and sporophyll types in various gymnosperms. A, branch of *Ephedra* with staminate cones; B, seedling of *Thuja gigantea*, showing stages in leaf development; C, vegetative leaves and staminate cones of *Taxus*, a single cone at right and a single sporophyll from a cone at the left; D, branch of *Torreya* with ovulate structure, and, E, branch with staminate structures, a single sporophyll at the left; F, leaves of *Agathis*, and, G, leaves of *Podocarpus*, both unusual forms among gymnosperms. (All except B drawn by Helen D. Hill.)

The genus *Tsuga* includes the hemlocks. They are evergreen trees with short flattened needles that appear to be definitely produced on two opposite sides of the branch or sometimes, in addition, on the top surface of the branch. At any rate, they form definite flat sprays that mark the genus as distinct from both the firs and the spruces. A leafstalk is present and is left as a roughening on the stem when the leaves fall, as in spruces. There is a single resin duct in the center of each leaf. The trunks are tall and straight and taper much less than do those of the spruces and firs. In trees up to fifty years of age, the slender tips of the leaders droop gracefully at the pointed crown of the tree and erroneously are said always to be drooped toward the east. Beyond this age, the crown of the tree becomes more rounded by a relatively larger growth of side branches than of the leader. The cones are small, especially in the eastern species, and pendent and in good seed years are produced in abundance over the entire crown of vigorous trees. Seeds are matured in one season. Commercially, the hemlocks are less important than any of the preceding conifers. West-

ern hemlock lumber is superior to the eastern coarse-grained and easily splintered wood, but this species has until recently been regarded as an inferior timber tree. Hemlock bark contains large quantities of tannin and has been much used in the tanning industry. Only four species of hemlock, two eastern and two western, are native to North America and their range is more limited than is that of the firs, spruces, and pines.

Pseudotsuga is a genus of false hemlocks (Figs. 269, A, 274). Its species are erroneously called spruces, firs, hemlocks, or pines, from all of which they differ in the peculiar three-pointed scale-like bracts that protrude from between the scales of the cone. The leaves are soft and flattened as in firs and hemlocks and not stiff and four-angled as in spruces. They are evergreen and possess two resin ducts as seen in cross section. A short but rather prominent stalk is left on the roughened branch when the leaf falls. Leaves come out from all sides of the stems as in the spruces. The cones are pendulous and mature their seeds the first season. But two species are known and only one (Douglas fir) is of great importance. The trunks of this species are tall and straight and reach a height rarely attained by any other American tree except the giant redwoods. Trees between 200 and 300 ft. high and 8 to 10 ft. in diameter are known, although these sizes are unusual. Old trees with bark as much as 2 ft. thick have been observed. Commercially, the tree is of great importance for lumber, though limited in its distribution to the Rocky Mountain region and westward and best developed in the humid Pacific Coast region of Washington and Oregon.

The genus *Larix* includes the true larches or tamaracks, although both of these names are frequently misapplied even in the lumber industry. In shedding their leaves every year, larches are distinct from all other American conifers except the cypress. The leaves are soft and flexible, 1 to 2 in. long and, except on the terminal twigs, they are produced in clusters of 10 to 40 on very short dwarf spurs on the branches. In some species, resin ducts are present and in others absent. The cones are pendent or suberect and mature their seeds in one season. Bristle-like, single-pointed bracts project from between the cone scales of some species. The larches are important timber trees. The wood is quite durable. But three or four species are known in America. They are trees of the colder parts of the north temperate zone. Both native and foreign species are occasionally used as ornamentals.

Taxodium is the genus that includes the bald cypress, of which two species, both southern in distribution, are known in the United States (Fig. 281). The leaves are usually not more than 1 cm. long, sometimes are very small and scale-like, and are deciduous. They are quite soft and appear to be arranged on two opposite sides of the stem, which, with the very fine branchlets on which they are borne, gives them a plume-like, or pinnate, appearance. The cones are rounded and about the size of a small walnut but the scales are closed so that the appearance is scarcely cone-like. The trunks are tapering and usually considerably enlarged at the base. Especially in sites subject to inundation, the roots develop peculiar conical upward hollow protuberances, the so-called "knees." These are as much as 4 to 6 ft. high and 2 to 4 ft. thick. The cypress is an important timber tree, producing soft, easily worked, and very durable wood. It is chiefly an inhabitant of swampy regions or overflow river bottoms.

The genus *Sequoia* includes the giant "big trees" (*Sequoia gigantea*) and the redwood (*Sequoia sempervirens*) of the Pacific Coast (Fig. 269, B). They are the only living species of the genus. The big tree probably attains the largest size, although heights of over 300 ft. are authentically recorded for both species. The diameter of such trees, 8 or 10 ft. above the swollen bases, may be as much as 20 or 30 ft., with a bark as much as 18 in. thick. The leaves of this species are slender, sharp pointed,

and somewhat scale-like, as in the eastern red cedar, while those of the redwood are flat, sharp pointed, and up to an inch in length. Both species are evergreen. The cones of the redwood mature in one year; those of the big tree during the second season. With the possible exception of some of the species of *Taxodium*, these are the longest lived of all living things, some of the big trees showing up to 2,300 annual rings. Probably the redwood is somewhat shorter lived, but trees with more than 1,000 annual



FIG. 281. Specimen of cypress (*Taxodium distichum*), with spreading trunk base, from Lake Providence, La.

rings are known. The big trees are known only in limited regions of central California on the western slopes of the Sierra Nevada mountains, but the redwood extends also into Oregon. The wood of both species is very durable, though soft, and, except that formed during the first 500 years, is close-grained. Prior to the glacial epoch, the species of *Sequoia* were as numerous and covered as wide a geographical range as any other genus of trees in the world. The species were almost destroyed during the Ice Ages so that only a remnant now remains. The petrified forests of the Yellowstone National Park are said to have been composed of species of this genus (Fig. 282). Their closest living relative is the bald cypress.

Libocedrus is the genus of the western incense cedar, found in California, Oregon,

and Nevada. The trees are evergreen with small, opposite, scale-like, overlapping, pointed leaves not unlike those of the red cedar. The smaller branches have the pressed appearance of arborvitae. The cones are very small and composed of only six or eight scales. The trunks taper upward and are much enlarged at the base. The wood is fragrant and extremely durable, though soft and light in weight. The limited range of the species and the great extent to which it is subject to heart rot render it of less importance commercially than it might otherwise be.

The red cedars, or junipers, belong to the genus *Juniperus* (Fig. 268). They are evergreen trees with either very small, scale-like, overlapping leaves or more needle-like, though short and sharp-pointed, leaves. Often both kinds of leaves are found on

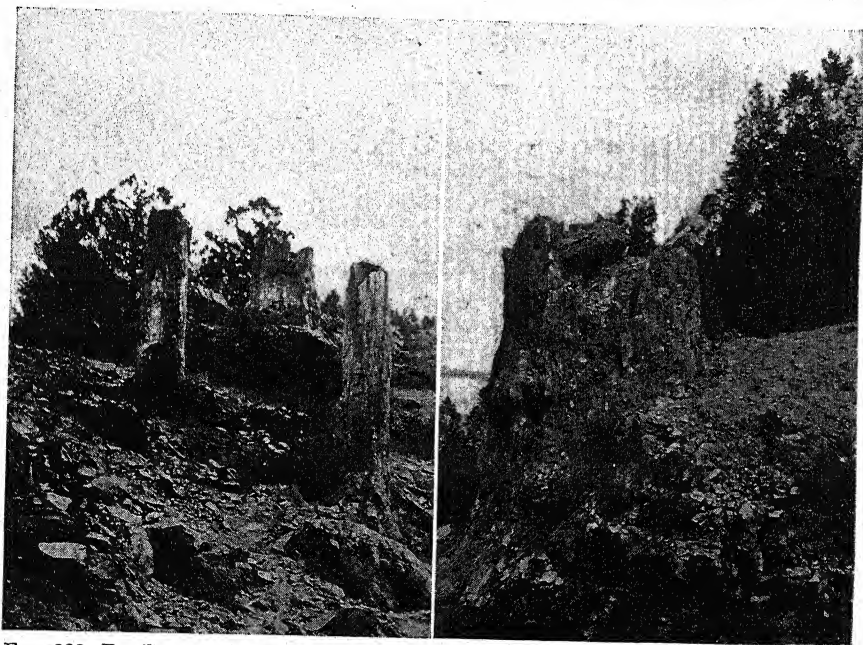


FIG. 282. Fossil trees identified as *Sequoia*, on Specimen Ridge in Yellowstone National Park, Wyo.

the same tree. The leaves have a pleasant odor. The ovulate cones, at maturity, are berry-like rather than cone-like and are blue or reddish in color and not larger than a small-sized pea. Morphologically they are cones in which the scales have become fleshy. American junipers are scarcely more than small-sized trees at their best and some are quite shrubby or prostrate in their growth. The wood is hard, close-grained, aromatic, and extremely durable, but the best of the trees are so small or so poorly formed that, as timber, their value is negligible. They are of some use, however, in cabinet work, in inlaying, and in pencil making. Eight or ten American species of *Juniperus* are known, widely distributed in the United States and Canada.

The western red cedar and the arborvitae belong to the genus *Thuja*. They resemble both the white cedar and the junipers. They differ from the junipers in the flat branches and in the possession of well-formed cones instead of berry-like structures. They differ from the white cedars (*Chamaecyparis*) in the elongated or el-

lipsoïd form of the cone and the broader twigs or branchlets ($\frac{1}{8}$ in.). Both the white cedars and *Thuja* have branchlets distinctly flattened as though pressed. The western red cedar is an important timber tree. The eastern arborvitae is of less importance, but both species furnish extremely durable timber. The western red cedar is still the most important source of shingles.

Several species of white cedar belong to the genus *Chamaecyparis*. They are difficult to distinguish from *Thuja*, but the cones are globose instead of elongated and the branchlets, while having the pressed appearance of species of *Thuja*, are considerably narrower ($\frac{1}{16}$ in.). The leaves are very small, scale-like, and overlapping. The cones mature their seeds in 1 year. The wood is close-grained and extremely durable, but the supply is limited and it is not extensively used except locally and to some extent in cabinet making. The single eastern species inhabits swamps of the Atlantic seaboard. The several western species are found in different habitats.

The genus *Taxus* (family Taxaceae) includes one western species, one eastern species, and one species in Florida. They are known as yews. The western species is a small tree with a maximum height of about 30 ft.; the eastern species is a straggling shrub; the southern species intermediate in size. The leaves are flat, less than an inch long, and their stalks are decurrent on the branches. They appear to grow on two opposite sides of the stem but actually are attached as well to the upper and lower surfaces, and by the twisting of the rather prominent leafstalks all leaves are brought into one horizontal plane. The outer covering of the seed, or arile, is fleshy and bright red in color.

OTHER GYMNOSPERMS

Although the species of the Coniferales constitute the dominant gymnospermous flora of the present, three additional orders of the gymnosperms have living representatives. These are the Cycadales, the Ginkgoales, and the Gnetales. Fossil remains indicate that all the living orders of gymnosperms were also represented in past geological periods. The Gnetales, however, are apparently very scantily represented by fossil remains. Such forms as have been found occur in more recent rock strata. It will be recalled that there are three orders of gymnosperms which are extinct and known only in fossil form. They are the Cycadofilicales, the Bennettitales, and the Cordaitales.

Order Cycadofilicales. The earliest fossil remains of seed plants are found in the strata of the Paleozoic age¹ and are estimated from various calculations to be from

¹ The different geological periods have been referred to so often in this and the following discussion that a table of these periods may prove of some assistance to the student.

GEOLOGICAL PERIODS	
<i>Era</i>	<i>Period</i>
Cenozoic	Recent } Quaternary
	Pleistocene }
	Pliocene }
	Miocene } Tertiary
	Oligocene }
	Eocene }
62	

100 million to 250 million years old. Among the oldest recognized seed plants are some that greatly resemble ferns, especially in their leaf forms. So great is this resemblance that they were at first thought to be ferns, but the discovery of seeds attached to the fern-like plants identified them as seed plants. Because of these features they are also called **pteridosperms**. Evidence is accumulating that these plants were not merely seed-bearing ferns. Studies of the epidermal tissues indicate closer similarities to gymnosperms than to ferns. Fossil remains indicate that the members of the Cycadofilicales or pteridosperms were plants usually with slender stems bearing large fern-like leaves that were widely spaced in spiral arrangement on the stem. That some of these plants were probably vine-like, climbing or sprawling types requiring support to maintain an upright position, is indicated by the slender stems and weakly developed vascular system. Some of the pteridosperms were sturdier and probably resembled the modern tree ferns. The mesarch condition typical of modern ferns is also found in the pteridosperms. Various of the fossil genera show stele types characteristic of the modern ferns. In *Heterangium* the primary wood of the stem occurred as a protostele; in a second type, *Lyginopteris*, there was a siphonostele; and a third genus, *Medullosa*, had a dissected siphonostele forming a typical dictyostele or polystele. Secondary wood and phloem tissues resulting from the activity of cambium were developed in all the stem types. Abundant development of sclerenchyma tissues was also a feature of most seed-fern stems. The occurrence of secondary wood and primitive fern types of steles presents a unique combination of traits.

Seeds were borne singly on the leaves. The position of seeds on the leaves varied. In some cases, thought possibly to be the most primitive arrangement, the seeds were produced on branched stalks that are reminiscent of the sporangia-bearing stalks of the Psilopsida. In other forms, the seeds were produced on the tips of the leaf pinules. In still other genera regarded as possibly more advanced, the seeds were produced on the surfaces of the leaves. The seeds were enclosed within cupules, which in some cases were fringed by the expanded bracts forming the structure.

Mesozoic.....	{ Cretaceous (Upper Cretaceous)
130	{ Comanchean (Lower Cretaceous)
	{ Jurassic
	{ Triassic
	{ Permian
	{ Pennsylvanian (Upper Carboniferous)
	{ Mississippian (Lower Carboniferous)
Paleozoic.....	{ Devonian
370	{ Silurian
	{ Ordovician
	{ Cambrian
Proterozoic	
500	
Archaean	
1,000	

The figures given under the eras represent computed millions of years that each of these eras lasted, as compiled by Dr. A. C. Noé and quoted by C. J. Chamberlain, "Gymnosperms, Structure, and Evolution," p. 3, University of Chicago Press, Chicago, 1935.

The Cycadofilicales flourished during the Carboniferous period of the Paleozoic era and possibly lived until the early periods of the Mesozoic era. They probably originated in the Devonian period although this is not exactly known, but fossils resembling seed ferns have been found in Devonian strata. Form, structural features, and reproduction indicate relationship of the pteridosperms with the ferns on the

primitive side and with the cycads on the more advanced side. Origin of the pteridosperms from the ancient ferns has been suggested. Since heterosporous ferns such as *Archaeopteris* are known to have existed in the Paleozoic era, the pteridosperms may have evolved from them. Another possibility is that they may have developed directly from plants associated in the Psilopsida group which flourished in the Devonian period. Regardless of the exact method of their origin, the pteridosperms are probably best regarded as seed plants belonging to the cycadophyte line of the gymnosperms and not as merely seed-bearing members of the fern plexus.

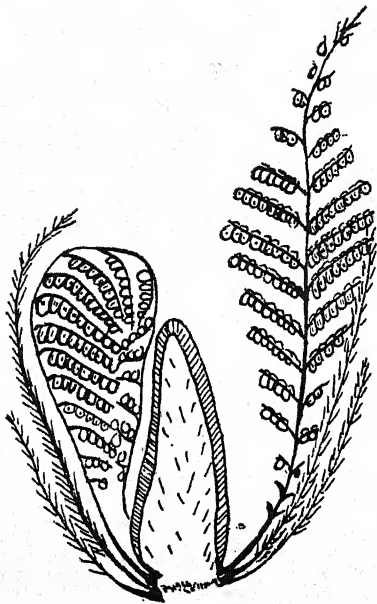


FIG. 283. *Cycadeoidea*. Diagrammatic sketch of longitudinal section through the bisporangiate strobilus. At the center is the apical cone closely invested by a zone of short-stalked abortive (?) ovules and interseminal scales. On the left is a single frond of the hypogynous staminate disk, with much reduced pinules bearing densely crowded sporangia. On the right a similar fertile frond is arbitrarily shown in an expanded position. Exterior to the fronds are the hairy bracts. About three-fourths natural size. (Redrawn from sketch by Dr. George R. Wieland, *Amer. Jour. Sci.*, 11: 424, 1901.)

Order Bennettitales or Hemicycadales. This group, often designated as the cycadeoids, are thought to have originated, like the cycads, from the Cycadofilicales. Long of world-wide distribution, they became extinct in the Mesozoic era. Some were short, thickset, stubby-stemmed, bearing large fern-like or palm-like leaves. Such stems ranged in height from a few inches to a meter and more. Others had small-bladed leaves and slender stems with the branching habit of the magnolias. They may even have been trees. The most significant feature of these plants was the fact that they were truly floral, producing both microsporophylls and megasporophylls in the same spiral structure. They thus formed a strobilus which was in actuality a

flower (Figs. 283, 284). The megasporophylls were aggregated in a compact cone in the center with the pinnate microsporophylls loosely surrounding it. These structures have been compared with the flower of the magnolia. The flower of the Hemicycadales differentiates them from both groups of plants to which they may be related, the Cycadofilicales, which produced staminate and ovulate strobili on the same plant, and the Cycadales, all known fossils and living species of which are dioecious (*i.e.*, producing staminate cones and ovulate cones on separate plants). During the Mesozoic age, when giant dinosaurs roamed the earth, these flowering cycads or cycadeoids flourished. Fossil evidence indicates that they were very widespread. They

have been found on all the continents. The Black Hills of South Dakota are the most famous collecting ground in the United States. These fossils have had the attention especially, in both field and laboratory, of Wieland, whose investigations afford most of the information concerning them.

Order Cycadales. The Cycadales are represented in the fossil flora of the early Mesozoic age and extend to the present time. Living cycads, represented by nine genera and perhaps 60 species, are but a remnant of a former abundant flora. The term "living fossils" has been applied to them. They are the most primitive living seed plants. In form they are usually short thick-stemmed plants, producing large fern-like leaves (Figs. 285, 286, 287), but some species attain heights of 50 or 60 ft. and are tree-like in form. The leaves of one genus, *Cycas* (Fig. 287), known as palm

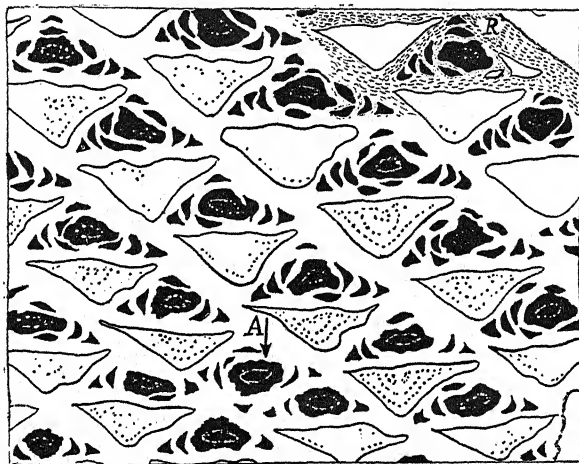


FIG. 284. *Monanthesia magnifica*. A cauliflorous cycadeoid from the Mesaverde upper Cretaceous of the San Juan Basin, northwestern New Mexico. Tangent section through armor of old frond bases with small flower stalk in each axilla except at A, where a frond base falls of later growth. The relation is nearly as persistent as that of bract and scale in a pine cone. The bundle patterns of the frond bases appear, likewise the bundle cylinder of the peduncles. The lower bracts are cut. At R is indicated the enveloping "raimentum" or chaff. (Figure and explanation by Dr. George R. Wieland.)

leaves to the floral trade, are extensively used in floral decoration. Cycads are indigenous to tropical and subtropical zones of both hemispheres and are much grown as ornamentals in all regions warm enough for their outside culture. Cycads live to great ages. Some are known to be a thousand years old.

Anatomically, the cycads show certain primitive features. Thus the leaves show the mesarch condition in the xylem of the veins. The stems have ectophloic siphonosteles. There is a large pith, a scanty wood region, and a large cortex region. The leaf bases remain and closely cover the stem. Although some cycads are branched, unbranched stems are characteristic of the group.

Cycad plants of the living species are definitely dioecious, the staminate and the ovulate cones being produced on separate plants. The microsporophylls are aggregated into relatively large staminate strobili, or cones. The megasporophylls vary in the several genera. They range from structures somewhat resembling leaves, which

are aggregated into a loose strobilus, as in the genus *Cycas* (Fig. 287), to highly modified and reduced structures aggregated into a compact cone, as in *Zamia*. Microspores and megaspores are developed as in the conifers, the microspores in spherical tetrads and the megaspores in linear tetrads. On germination, the microspores give rise to



FIG. 285. A cycad, *Macrozamia Moorei*, native in Australia. (Photograph by Dr. C. J. Chamberlain.)

male gametophytes and the megaspores to female gametophytes. Usually only one megaspore of the tetrad develops, giving rise to a single gametophyte in each ovule.

The gametophytes of the cycads are developed much like those of the conifers but differ from the latter in many important details. The mature female gametophyte consists of a mass of tissue within the nucellus and the integuments of the ovule. About four or five archegonia are formed, each consisting of two neck cells, a ventral canal cell, which usually disorganizes early, and an egg (Fig. 288). In the development of the male gametophyte, the microspore, or pollen grain, by a series of divisions,

forms first a prothallial cell, a tube cell, and a generative cell. The prothallial cell does not disorganize as do the prothallial cells of conifers but persists throughout the life of the male gametophyte. The pollen is wingless and is shed in the three-celled stage of the gametophyte (Fig. 289). Cycads are wind-pollinated. When the ovule is reached, the tube cell forms a pollen tube which begins to grow through the nucellus. The action and function of the pollen tube of cycads are entirely different from those of

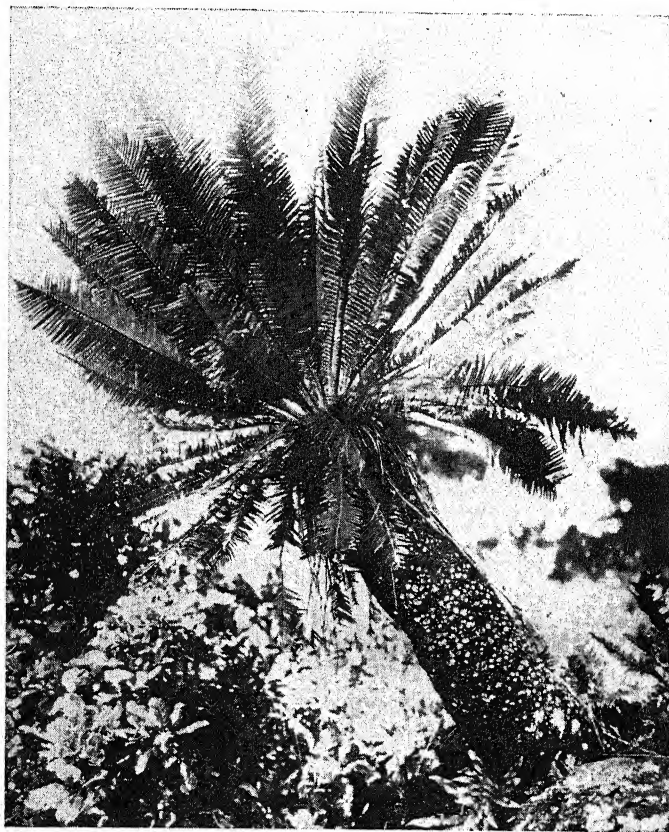


FIG. 286. *Dioon edule*, a cycad growing at Chavarrillo, Mexico. (From C. J. Chamberlain, "Elements of Plant Science," Fig. 257, p. 288, McGraw-Hill Book Company, Inc., New York, 1930.)

pollen tubes in conifers. The function of the pollen tube in cycads is apparently entirely one of nutrition. It penetrates and disorganizes the tissues of the nucellus, but it does not carry the male cells to the archegonium as does the pollen tube in conifers.

By the growth of many pollen tubes, the cells of the nucellus are broken down and the tissue often completely disorganized above that region of the female gametophyte containing the archegonia. The further development of the male gametophyte consists of the division of the generative cell to form a stalk cell, which takes no further



FIG. 287. Cycads (*Cycas revoluta*). Two to the right show megasporophylls grouped into the ovulate cones. (Photograph furnished by Conservatories of the New York Botanical Garden.)

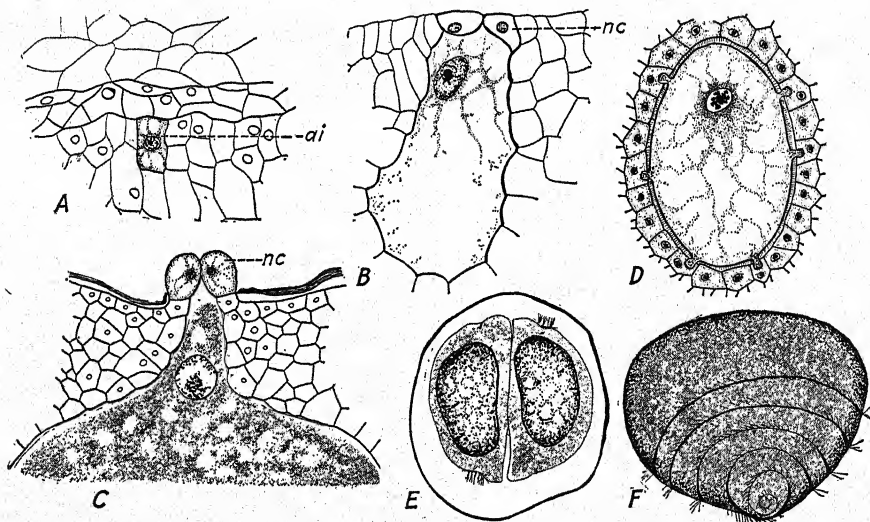


FIG. 288. Development of archegonium and sperms in cycads. A-D, archegonia; A, archegonial initial, *ai*, below a nutritive layer; B, young archegonium showing central cell and two neck cells, *nc*; C, older stage with nucleus preceding division into egg and ventral nuclei; D, mature archegonium, cut to one side, showing egg with nucleus and haustoria extending into surrounding jacket cells; E, sperms within body cell; F, ciliate sperm.

part in the development, and a body cell. The body cell, by division, forms two male cells, or sperms, each with a coiled structure called a **blepharoplast** bearing hundreds of cilia (Figs. 288, *E*, *F*; 289, *I*, *J*). The ciliated motile sperm of the cycads is one of their most primitive features. The sperms swim about in the liquid within the pollen chamber and finally penetrate the neck of the archegonium. Fertilization is accomplished by fusion of the sperm nucleus with the egg nucleus.

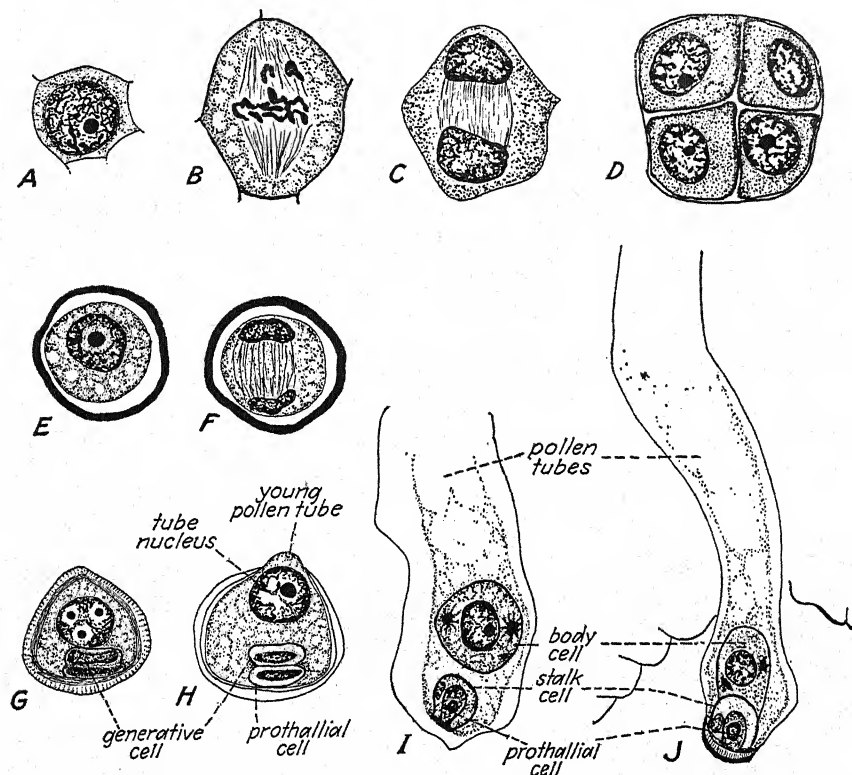


FIG. 289. Development of microspores and male gametophyte of a cycad. *A*, microspore mother cell; *B*, metaphase, and, *C*, telophase of first maturation division; *D*, tetrad of microspores; *E*, microspore; *F*–*H*, stages in development of pollen grain from microspore; *I*, *J*, nearly mature pollen tubes.

Repeated division of the fertilized egg without wall formation results in the formation of hundreds of free nuclei within the archegonium. This constitutes the early stages of the embryo and is similar to the early embryonic stages in the conifers. Eventually walls begin to appear in the embryo and the long suspensor and the embryo proper begin to be differentiated. At maturity, the embryo develops two cotyledons.

The outer covering of the seeds of cycads consists of three layers, a middle stony layer and the inner and outer fleshy layers, both of which are supplied with vascular bundles. The outer fleshy layer dries up and adheres tightly to the hard middle layer, forming a hard type of seed.

Order Ginkgoales. The *Ginkgo* tree, native in China, though wholly unknown in the wild state, is the only living representative of the order Ginkgoales, an order which flourished with numerous genera and species throughout the Mesozoic age. This tree, now widely cultivated as an ornamental tree, has, in fact, an unbroken history far back into past geological ages. Scarcely any other living plant so completely fulfills the name of living fossil as does the *Ginkgo*.

The *Ginkgo* resembles the conifers. It is a large, tall, peculiarly handsome, branching tree frequently with a central shaft (Fig. 290). The leaves, which are two-lobed, have dichotomously branched veins (Fig. 291). The venation has the superficial appearance of being parallel. The common name "maidenhair tree" refers to the

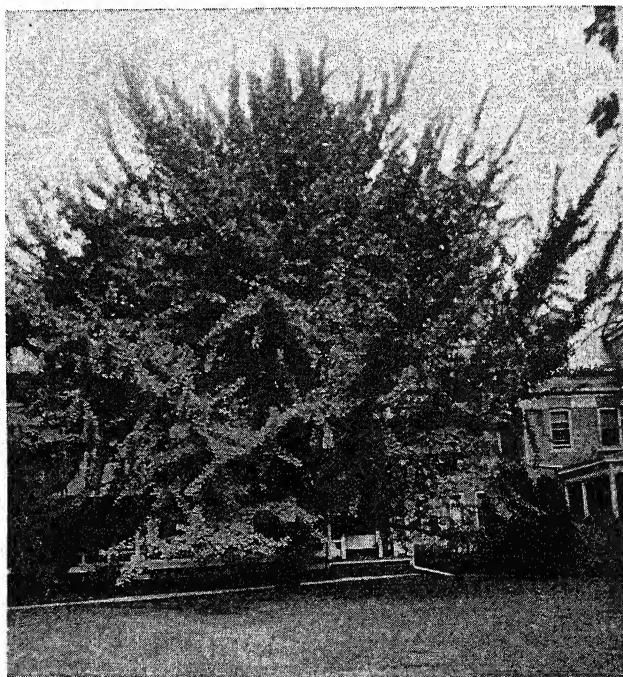


FIG. 290. *Ginkgo* tree on campus of the Pennsylvania State College, State College, Penn.

striking resemblance of the leaves to those of *Adiantum*, the maidenhair fern. There are long branches which bear scattered leaves and short branches which bear clustered leaves and produce the reproductive structures. The short branches resemble the fruit spurs of the apple. The trees are of two kinds, one bearing only staminate strobili and the other only ovulate strobili. The staminate strobili are loose catkin-like structures and the microsporophylls and sporangia are of a primitive type. The ovulate strobili take the form of long, slender, fused stalks bearing single ovules (Fig. 291). Normally, there are but two of the stalks bearing two seeds set near together; but stalk clusters in threes and even up to six and seven occur.

The gametophytes of the *Ginkgo*, although they are slightly more primitive than

those of members of the Cycadales, follow the general lines of development of the latter (Fig. 292). The microspores develop into pollen grains which are shed at the four-celled stage. In the mature pollen grain there are two prothallial cells, one disintegrating and one persistent, a tube cell and a generative cell. After pollination, the male gametophyte continues its growth and development in the tissues of the nucellus. The pollen tube, as in the cycads, acts as a haustorium. The generative cell divides, producing the stalk cell and the body cell, the body cell producing two motile sperms, characteristic of primitive gymnosperms.

The female gametophyte, early a multinucleate structure without cell walls, eventually develops into an ovoid mass of tissue, producing two or three archegonia.

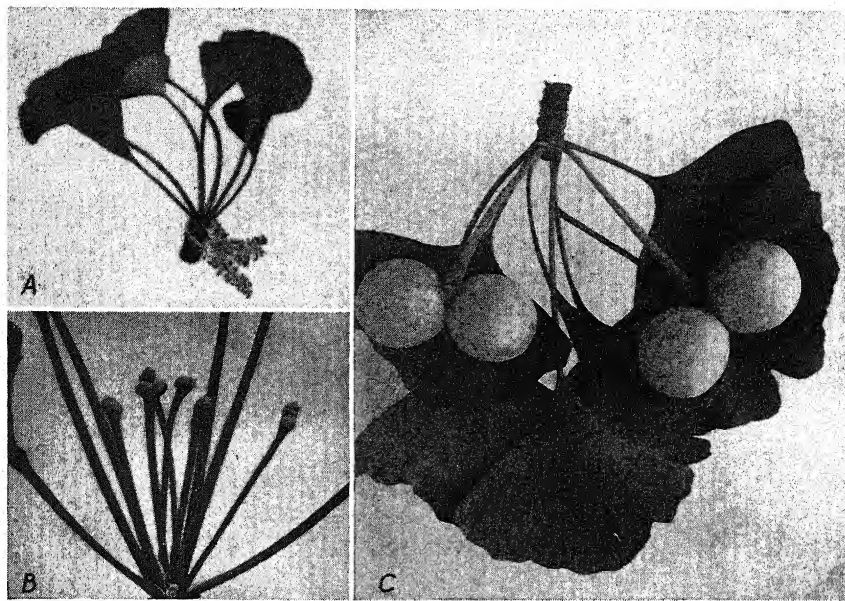


FIG. 291. Reproductive structures of *Ginkgo biloba*. A, the staminate strobili at about the time pollen is shed; B, young ovules as they appear at the time the staminate strobili are in the stage shown at A; C, mature ovules developing seeds. (Photographs of A and B by D. S. Wright.)

A peculiar feature of the female gametophyte of *Ginkgo* is the development of a vertical mass of tissue between the archegonia. The archegonial chamber surrounds this elevated mass of tissue. The archegonia have two neck cells, a ventral canal cell cut off by a cell wall, and the egg nucleus surrounded by abundant cytoplasm. Because of the presence of a wall separating the ventral canal cell from the egg, the archegonia of *Ginkgo* are regarded as being more primitive than those of the cycads. One of the motile sperms penetrates an archegonium and its nucleus fuses with the egg nucleus. The fertilized egg develops the embryo. There is an early free nuclear stage consisting of 256 nuclei without cell walls which is followed by wall formation. In the later stages of the embryo, root, stem, and cotyledons are differentiated with the suspensor poorly developed. The ovule of *Ginkgo* ripens into a seed, in which the middle layer

of the integument becomes hard and the outer layer soft and fleshy. The seed of *Ginkgo* bears a superficial resemblance to a drupe fruit, but the two structures are in no sense homologous (Fig. 291).

Order Gnetales. The Gnetales, compared with the other orders of gymnosperms, is a modern group, consisting of three genera, *Ephedra*, *Welwitschia*, and *Gnetum*. These genera, apparently not closely related, comprise a group of plants which although

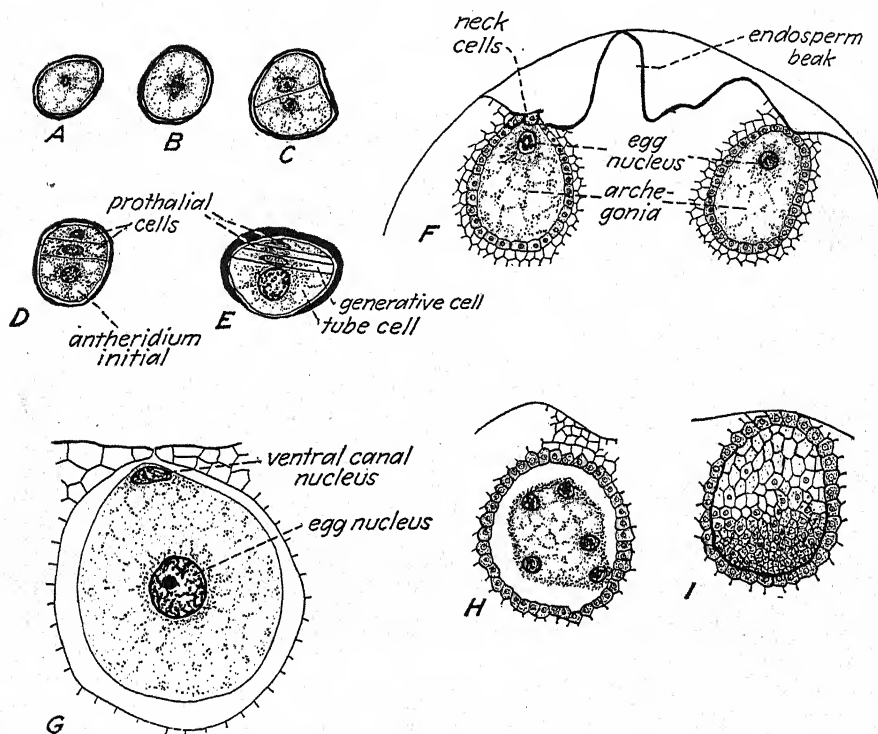


FIG. 292. Gametophytic and embryonic structures of *Ginkgo*. A-E, early stages in development of male gametophyte; A, microspore; B, C, early stages in development; D, three-celled stage; E, mature pollen grain; F, micropylar end of female gametophyte; G, older stage; H, free nucleate stage of young embryo; I, proembryo with small cells at apex. (Drawings except E and G by Helen C. Deuss.)

undoubtedly gymnospermous is of uncertain relationship. The plants are diverse in every respect: in form, in habitat, in distribution, and in the morphological details of reproduction. *Ephedra*, a bushy or trailing plant, developing only scale leaves, grows in the dry regions of both hemispheres (Figs. 280, A; 296). Some of the species grow in Mexico and the southwestern region of the United States. *Welwitschia* is restricted to the dry regions of South Africa. The plants of *Welwitschia* are very peculiar. The stem is a blunt, tuberous structure, tapering into a long taproot. Only two leaves are produced. These leaves, renewed by a basal meristematic region,

are described as split into long, leathery ribbons by the force of the wind (Fig. 293). The species of *Gnetum* are mostly vines, producing large netted-veined leaves resembling those of the dicotyledons. Some species of *Gnetum* are tree forms. *Gnetum* is native in the moist tropical forests of Asia, Africa, and South America.

Anatomically, the Gnetales have a combination of the typical gymnospermous tracheid with bordered pits and a type of vessel, or tracheal tube, resembling the vessels of the xylem of angiosperms. The development of the vessel indicates a high evolutionary position as regards the anatomical features of the group.

The Gnetales are dioecious, although there is a tendency to produce both microsporangia and megasporangia together in some instances. The strobili greatly resemble the more simple types of angiospermous flowers (Figs. 280, A; 293). The principal feature of the strobili of Gnetales is that both staminate and ovulate strobili are compound. The ovulate strobilus of the conifers is compound, but in the Gnetales the staminate strobilus as well as the ovulate strobilus is composed of bracts and sporophylls. All the Gnetales produce naked ovules, which, regardless of other advanced anatomical and reproductive features, characterizes them as gymnosperms.



FIG. 293. *Welwitschia*. Left, young plant showing leaves and broad, flattened stem with cones on short branches; right, old plant, showing conditions of the leaves after exposure to the elements for a number of years. (Photographs by Prof. W. P. Thompson.)

The details of reproduction in the Gnetales vary with each of the genera. *Ephedra* does not advance beyond the type of reproduction characteristic of other living gymnosperms (Fig. 294). It has a female gametophyte producing archegonia. *Welwitschia* and *Gnetum*, however, do show advances over other gymnosperms in their reproductive structures. Neither of these genera develops archegonia. In the case of *Gnetum*, there is a female gametophyte resembling the embryo sac of the angiosperms. At maturity, it is partially in the free nuclear condition. In this genus, one of the free nuclei in the female gametophyte functions as an egg, paralleling in this respect the situation in the angiosperms in which the egg is a free nucleus without an organized cell with a cell wall.

In *Ephedra* and *Welwitschia*, the male gametophytes remain on the typical gymnosperm level as indicated by the development of prothallial cells. In *Ephedra*, there are one cell and one free nucleus. In *Welwitschia*, apparently a single prothallial nucleus without a cell wall is produced. *Gnetum*, however, produces no prothallial cells or free nuclei. In this feature of its reproduction it also almost reaches the angiosperm level. The pollen grains have only three nuclei. It retains its gymnosperm standing in that the generative cell forms a stalk cell and a body cell, the latter

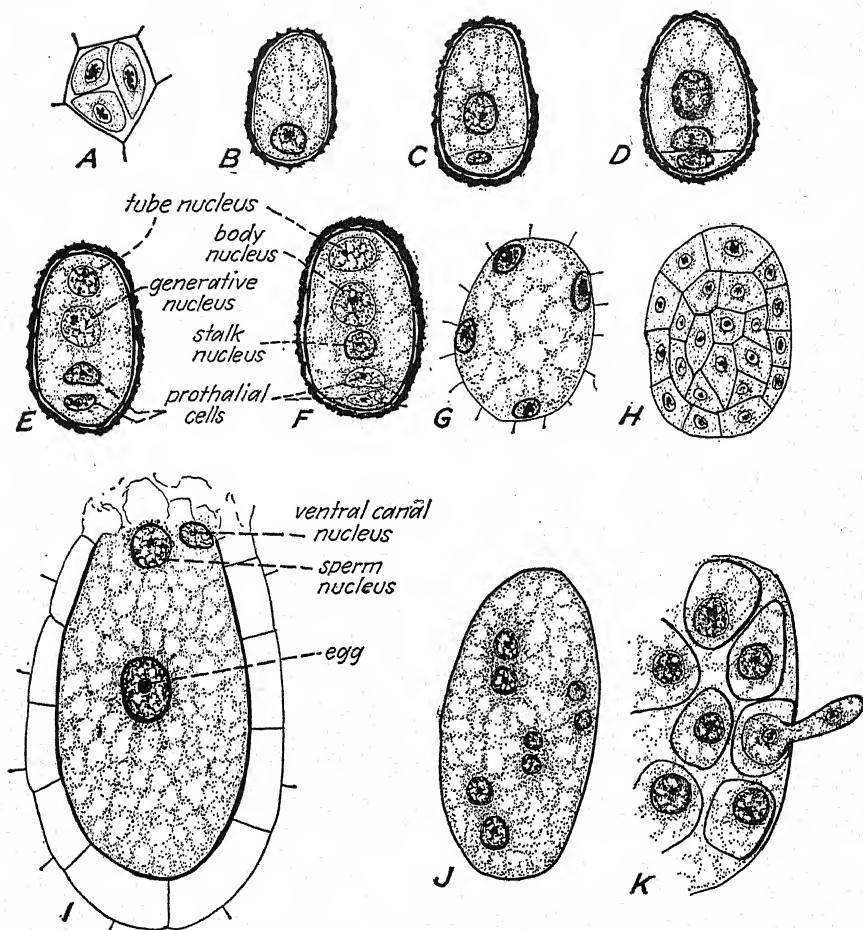


FIG. 294. Gametophytic and embryonic structures in *Ephedra*. A-F, stages in development of male gametophyte beginning with tetrad of microspores, A; B, single microspore or pollen grain; C-F, successive stages resulting finally in F, the male gametophyte; stage E shows the generative nucleus before it has divided to form the body nucleus and the stalk nucleus; the final stage, in which the body cell divides to form the sperms, is not shown; G, young female gametophyte with four free nuclei, parietally placed; H, female gametophyte somewhat older; I, archegonium with egg and ventral canal nucleus; a sperm nucleus is entering the archegonium; J, eight free nuclei in embryo; K, tubular elongation of one of proembryonal cells with divided nucleus. (Drawings by Helen C. Deuss from slides prepared by Dr. W. J. G. Land.)

forming the two male cells. This is one cell division more than is found in the angiosperms.

While the Gnetales approach the angiosperms in both anatomical and reproductive features, it is doubtful if they represent the ancestors of the angiosperms. The principal reason for this doubt lies in the fossil remains. Angiosperms antedate the Gnetales in the fossil records.

ANGIOSPERMS

General Features. The angiosperms, commonly known as the flowering plants, are recognized as the higher seed plants in contrast to the gymnosperms, or lower seed plants. The flower, the feature which characterizes the entire group, shows great diversity (Figs. 105, 295). Several other prominent characteristics distinguish the angiosperms from the gymnosperms, which often bear their reproductive organs in cones. In the angiosperms, the ovules, which mature into seeds, are produced on sporophylls, or carpels, which grow into some kind of closed structure. The angiosperms are thus said to produce **enclosed seeds**. The gymnosperms bear their seeds *on open scales*. The leaves of angiosperms are generally large

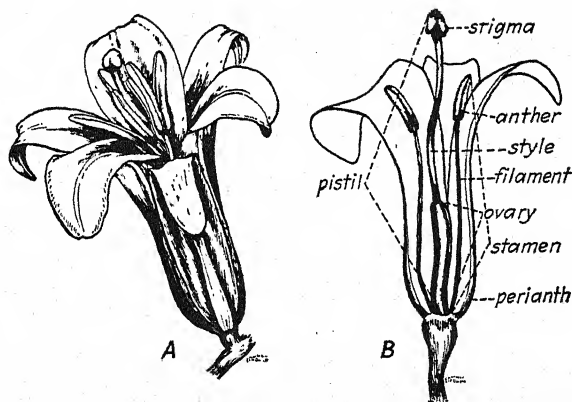


FIG. 295. Flowers of the lily, one of the monocotyledons. A, general view of the flower, showing the parts; B, longitudinal section of the flower, showing parts of the perianth, stamens, and pistil with its parts. (Drawings by Elsie M. McDougale.)

and broad in contrast with the frequently small, needle-like leaves of many modern gymnosperms. The structure of the xylem tissues of angiosperms and gymnosperms differs in anatomical details. The conducting tissues of the xylem of gymnosperms are composed of tracheids, single-celled structures. The angiosperms typically have vessels, composed of segments derived originally from single cells but at maturity fused into long, continuous tubes. The class Angiospermae, a large and diverse group of plants, is divided into two subclasses the Monocotyledoneae, or monocotyledons, and the Dicotyledoneae, or dicotyledons. The monocotyledons contain about 25,000 species which are grouped into 45 families and 11 orders. The dicotyledons are grouped into 40 orders, 230 families, about 6,000 genera, and more than 100,000 species.

The monocotyledons are a group of plants of great economic importance to mankind (Fig. 296). Many prominent food plants, such as the bananas

and all the cereals and grasses, including corn, wheat, rice, barley, and oats, belong to this group. In addition, lilies, tulips, orchids, and many other common flowering plants are monocotyledons. The monocotyledons have definite structural and morphological characters by which they can easily be distinguished from the dicotyledons. The embryo of the monocotyledons contains but a single cotyledon which bears little resemblance to the more familiar cotyledons of dicotyledonous plants (Figs. 302,

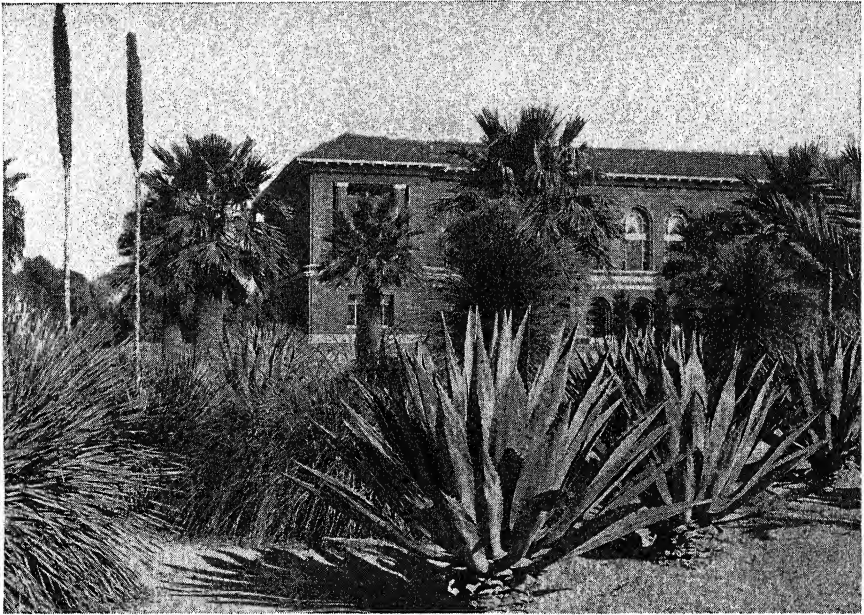


FIG. 296. A group of xerophytic plants, mostly monocotyledons. In the center foreground and to the right are three specimens of the *Agave* or century plant. The background in front of the building is occupied by palms. An *Ephedra*, one of the Gnetales, occupies the left center. (Photograph furnished by Dr. A. F. Hemenway.)

303). The leaves are nearly always parallel-veined, and the tips of the veins are united into a continuous vascular circuit. The organs of the flower are usually in threes or some multiple of three, as three sepals, three petals, three or six stamens, and three carpels. Though a few monocotyledonous plants, such as some of the palms, are fairly large trees, many of the monocotyledons are grass-like or small herbaceous plants.

The dicotyledons constitute the largest group of seed plants. The characteristics of the group are the development of two cotyledons in the embryo; generally netted-veined leaves with the veins and their branches ending free in the mesophyll of the leaf; and the flower parts usually in

fours or fives or multiples of these numbers. Many forest trees, as, for example, the oak and the maple and most of the fruit trees, including apple, orange, pear, peach, and plum, are dicotyledons. Beans, peas, and potatoes constitute the principal dicotyledonous food crops. A great number of the ornamentals, such as roses, geraniums, asters, mints, and snapdragons, are dicotyledons.

Since the angiosperms are a very large group of plants, growing in all kinds of situations and under all climatic conditions, they present great variation in size, form, structure, and reproductive features. In size, angiosperms vary from minute forms such as *Wolffia*, which is only a small fraction of an inch in diameter, to giant forest trees. Every structural feature varies, leaves and flowers being especially diverse in size, form, and structure. Anatomically, the stem structures are extremely diverse, particularly among the dicotyledons. Though certain reproductive structures distinguish the group as a whole, these too show great variation. With such diversity in a large group of plants, it is scarcely possible to select typical structures for description. Just what would be a typical flower or leaf or stem or fruit or method of reproduction would be difficult to decide. In the discussion of these matters it should be emphasized that the plants which are selected for study are merely the most available or best known and not necessarily the most typical.

Relative Importance of Sporophyte and Gametophyte. In the angiosperms, as in most of the vascular plants, the sporophytic structures attain greater size than the gametophytic structures. The recognized plant, consisting of roots, stems, leaves, and the flowers with all their conspicuous parts, sporophylls and sporangia, and finally the mature fruit, constitutes the sporophyte, or diploid ($2N$), structures. The nuclei of the cells of all tissues making up these structures have the diploid number of chromosomes.

The gametophytic structures in the angiosperms attain the greatest degree of reduction in size found anywhere in the plant kingdom. The gametophytes, or haploid tissues, are microscopic structures developed following the maturation processes and are best described later.

Anatomy of the Angiosperms.¹ The outstanding anatomical feature of the angiosperms common to both dicotyledons and monocotyledons is the presence of vessels in the xylem. In the gymnosperms, vessels are known in only one order, the Gnetales. Vessels, then, are a representative feature of the angiosperms. A vessel is composed of a vertical series of cells with their end walls resorbed, resulting in the formation of a continuous open channel for the passage of water.

While the monocotyledons have many structural features in common with the

¹ Attention is directed to the anatomical discussion in Part I where a detailed account of the structural features of the angiosperms may be found.

dicotyledons, they differ anatomically in certain respects. In the stems of monocotyledons, the vascular bundles in general have a "scattered" arrangement. Each bundle is of the closed type; *i.e.*, there is little or no persistent cambium and therefore, in general, all the tissues of the monocotyledons are primary tissues. A very few monocotyledons are exceptional in that a very weak cambium develops in the stem with the production of a small amount of secondary tissue. The individual bundles of the monocotyledons are of two types, amphivasal bundles with a central core of phloem surrounded by a cylinder of xylem, and collateral bundles with the xylem and phloem on the same radius. The lack of a cambium cylinder in the monocotyledons is related to the lack of secondary wood in the group.

The bundles of the stem of the dicotyledonous plant are arranged in the form of a cylinder with the pith in the center. A transverse section of such a stem shows the bundles in a circle around the pith. This is the typical ectophloic siphonostele. The dicotyledons are characterized anatomically by the presence of collateral endarch bundles. That is, in these bundles the protoxylem points of the primary xylem are located toward the center of the stem and differentiation of the metaxylem is toward the outside. Collateral bundles are those with the xylem and phloem on the same radius, with the xylem located toward the center and the phloem toward the circumference of the stem. In most species an active cambium cylinder is present, and in the case of woody plants a heavy cylinder of secondary wood is laid down each year. Since the cambium passes through each bundle, it has the capacity for indefinite growth. Such bundles are called open bundles.

On the basis of anatomical characters, dicotyledons may be differentiated as herbaceous or woody. Herbaceous plants have relatively large pith and cortex and relatively little wood or xylem. Woody plants have relatively little pith and cortex and a relatively large amount of xylem. Woody plants may live for many years, while herbaceous plants are generally short-lived. Vines and climbing plants are distinguished by a relatively small development of xylem, and their bundles are generally separated by large rays. The bast fibers are well developed and generally abundant. The whole anatomical development in the stems of vines is well adapted to the climbing habit.

The Spore-bearing Structures. The stamens and carpels (Figs. 105, 295), the spore-bearing structures of the angiosperms, can be compared morphologically with the sporophylls of the gymnosperms, *Selaginella*, and the fern. The stamens of the angiosperms are homologous with the microsporophylls of the staminate cones of the pine and spruce, with the microsporophylls of the bisporangiate cone of *Selaginella*, and finally with the fertile leaves or sporophylls of the fern. The carpels of the pistil of the angiosperm flower are homologous with the megasporophylls of the ovulate cone of the pine and the spruce, with the megasporophylls of the bisporangiate cone of *Selaginella*, and also with the fertile leaves of the fern.

The microsporangia are produced in the anther, or pollen sac, at the top of the stamen. In a young anther, there are four narrow, elongated masses of spore-bearing, or sporogenous, tissue. In transverse section these appear in four lobes of the anther (Fig. 105). Later they appear as two masses of sporogenous cells, one on each side of the mature anther.

Dehiscence results from the activity of special cellular mechanisms (Fig. 105).

The ovule, which is a megasporangium enclosed by the integuments, is produced in the carpel. The carpels are fused together, forming the pistil.

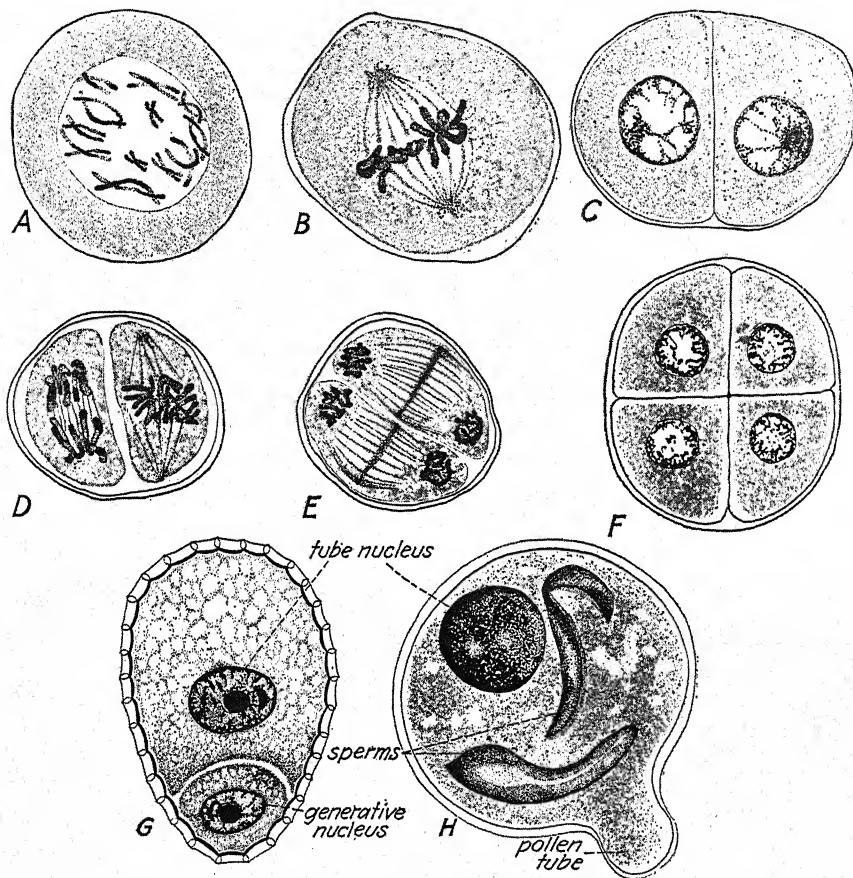


FIG. 297. Maturation of microspores and germination of pollen grains of angiosperms. A, prophase, and, B, metaphase of first division of the microspore mother cell; C, diad; D, metaphase and anaphase of second division; E, telophase of second division; F, resulting quartet of microspores; G, pollen grain of lily; H, early stage in the germination of a pollen grain of chrysanthemum daisy. (G and H drawn by Helen D. Hill.)

The ovules are produced in that portion of the carpel known as the ovary and are attached to it by a specialized tissue known as the placenta. Differences in methods of attachment are used as criteria of identification in taxonomic work. The ovules are attached to the placenta by a stalk called the funiculus. The ovules may be erect, with the stalk at the base, or half

inverted, with the axis of the ovule perpendicular to that of the stalk, or they may be completely inverted on the stalk, with the axis of the ovule parallel to that of the stalk.

The coverings, or integuments, of the ovule arise as a collar-like mass of tissue at the base of the young megasporangium and grow over and around it, completely covering it, with the exception of the micropyle (little gate) at the tip. Later in the development, pollen tubes may enter through the micropyle and penetrate the tissues of the megasporangium.

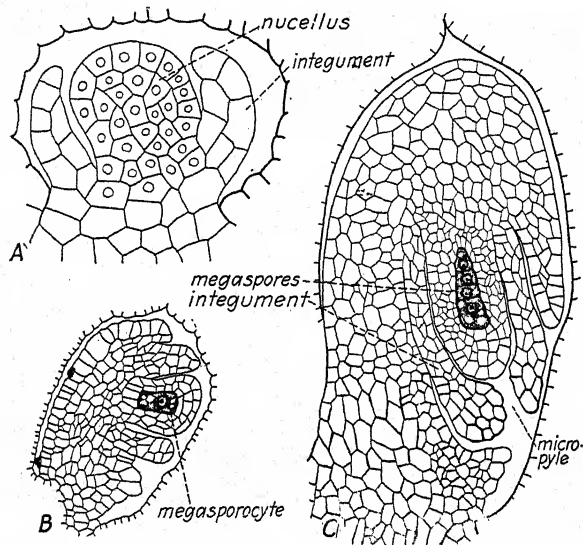


FIG. 298. Young ovules of *Carex*. A, very young ovule with undifferentiated nucellus and integuments; B, ovule with integuments; the megaspore mother cell has been differentiated within the nucellus; C, ovule with integuments and micropyle. Four megaspores in linear arrangement have been developed as a result of the maturation divisions in the megasporocyte. (Drawings by Helen D. Hill.)

Diversity in the details of structures concerned with reproduction, and variation in some of the minor features of the methods of reproduction, are found throughout the angiosperms. This diversity is found in the development of the anther, in the details of behavior in the differentiation of the microsporocytes, and the production of the microspores during the maturation processes. Similar diversity is found in the structure of the ovules with variation in a number of features of the megasporocytes, in the nucellus, or megasporangium within the ovule. The maturation processes take place in the microsporocytes in the anthers and in the megasporocytes in the ovules. During these maturation processes the number of chromosomes is reduced from the diploid to the haploid number and, therefore, the male gametophytes and the female gametophytes are ini-

tiated at this time. The maturation processes follow the usual course of events. Meiosis occurs in the microsporocytes. As a result of these two divisions, the diploid nucleus of the microsporocyte is divided into four haploid nuclei (Fig. 297, *F*). Walls form around these nuclei and the resulting four cells mature into a group of four microspores, each of which eventually develops by a process of growth and nuclear division into a pollen grain.

In many genera, the maturation processes in the megasporocyte, or megaspore mother cell, within the nucellus of the ovule result in the production of four distinct cells usually arranged in a row or in the form of a linear quartet (Figs. 298, *C*; 299, *F*). These four cells resulting from meiosis contain the haploid number of chromosomes and are the four megaspores. They are homologous and correspond with the megaspores found in the ovules of the pine of the gymnosperms and the megaspores in the sporangia of *Selaginella* and other of the heterosporous forms. Only one of the megaspores normally functions in the production of a female gametophyte. The other three die and disintegrate (Fig. 299, *G*). The megaspore situated farthest from the micropyle is usually best located as regards the food supply and generally functions to produce the female gametophyte.

Certain plants vary from the foregoing methods of formation of the megaspores and female gametophytes. The variations are based upon the number of divisions which occur in the formation of these structures. Sometimes only three megaspores are formed, owing to the fact that but one of the haploid cells divides, following meiosis.

The Gametophytes. The gametophytes of the angiosperms begin with the megaspores and microspores, respectively, which are the products of the maturation processes during which the reduction in chromosome number has occurred. The names "mega" (large) and "micro" (small) applied to these spores implies that there is a difference in size of the spores. In some instances, there is a difference in size of mega- and microspores in the angiosperms; in many cases, however, there is actually very little difference in the sizes of megaspores and microspores of the angiosperms and many gymnosperms as well. The names indicate rather comparisons with the large and small spores of other heterosporous plants than an actual difference in size. The mature gametophytes produced by the germination and growth of the megaspores and microspores are extremely reduced structures compared with those of the lower plants. The function of the gametophytes, however, remains the same, *i.e.*, the production of gametes capable of entering into fertilization.

The female gametophyte is developed entirely within the wall of the megaspore located in the ovule. The functional megaspore, generally the lowest one of the row of four, enlarges and by a series of ordinary mitotic

nuclear divisions develops into the mature gametophyte. The nucleus of the megaspore divides, forming two nuclei without the production of cell walls. The two nuclei divide again, forming four, and the simultaneous

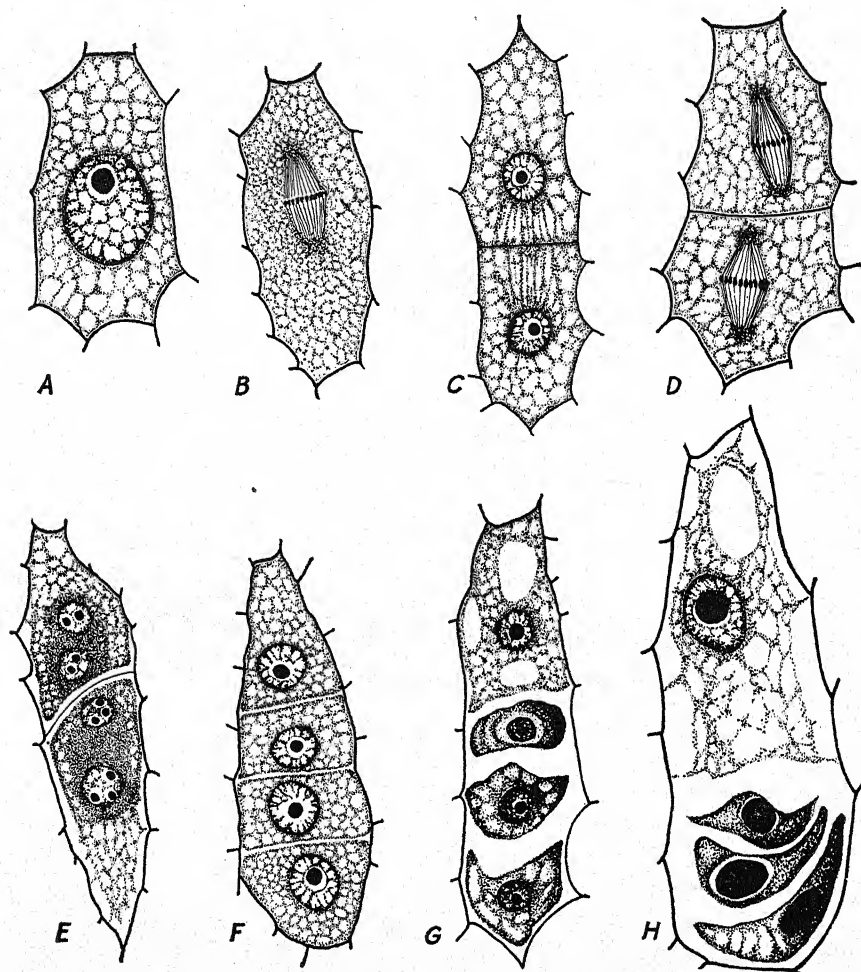


FIG. 299. Development of the megaspores of *Carex*. *A*, the megaspore mother cell as shown in the ovule in Fig. 298, *B*; the nucleus is a diploid structure; *B*, metaphase of the first maturation division; *C*, diad; *D*, metaphase of second maturation division; *E*, four haploid nuclei of the megaspores; *F*, the haploid megaspores, shown also in Fig. 298, *C*; *G* and *H*, enlargement of the functional megaspore and early disorganization of three nonfunctional megaspores toward the micropylar (lower) end of the ovule.

division of each of these results in the production of eight nuclei within the original wall of the megaspore. These eight nuclei contain the haploid number of chromosomes and without separating walls are free in the cyto-

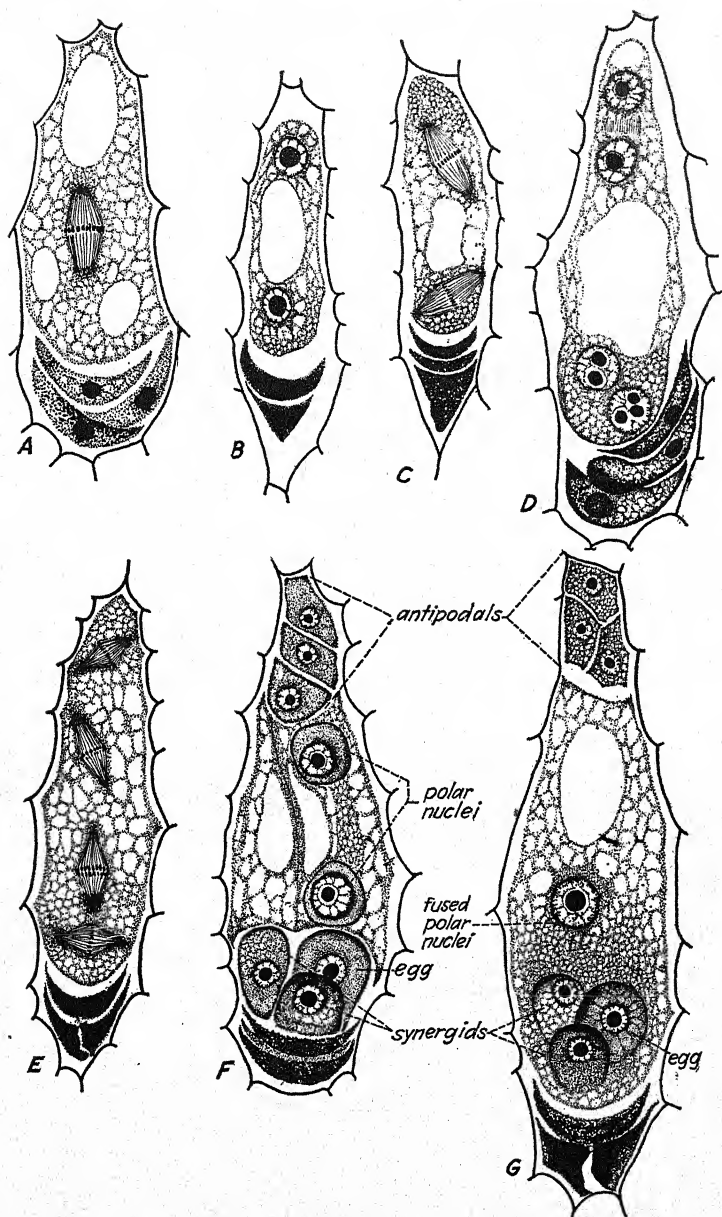


FIG. 300. Development of the female gametophyte of *Carex*. Beginning with *G* of Fig. 299, three of the four megaspores have degenerated, shown at the micropylar (lower) end; *A-E*, division of the functional haploid megaspore into two, four, and finally, in *F*, eight haploid nuclei with the three antipodal nuclei, two polar nuclei, two synergids, and egg nucleus; *G*, nuclei organized into the mature female gametophyte.

plasm common to all (Fig. 300). Usually there are four nuclei at each end of the female gametophyte, or "embryo sac." This structure is developed from the enlarging megaspore. The mature female gametophyte is organized from these eight nuclei. One nucleus from each end of the embryo sac migrates toward the center (Fig. 300, *F*). These two are termed the **polar nuclei**, *i.e.*, one from each pole of the sac. They eventually fuse and take part in the development of the endosperm.

The **female gamete**, or **egg**, is developed from one of the three nuclei remaining at the part of the embryo sac nearest the micropyle. This egg cell, together with the two remaining nuclei, called the **synergids** (or helpers), constitute what is frequently referred to as the **egg apparatus**. The three nuclei at the end of the embryo sac farthest from the micropyle

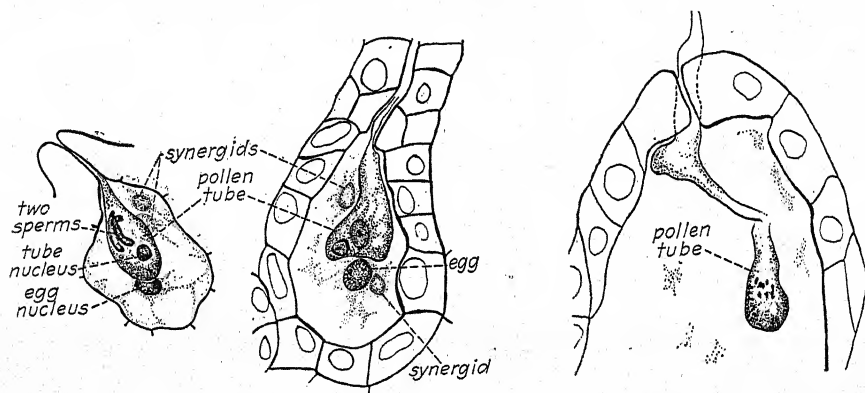


FIG. 301. Development of the pollen tube. *A*, *Cypripedium*, or lady slipper, one of the orchids; pollen tube with two male cells or sperms entering the embryo sac; *B*, *Cypripedium*, pollen tube entering the embryo sac; *C*, pollen tube of *Lilium* entering embryo sac; nuclei of embryo sac not shown.

are termed **antipodals** (opposites) and generally remain functionless although they may sometimes develop some tissue. The mature female gametophyte in most of the common angiosperms that have been studied consists of seven cells, *viz.*, the egg, two synergids, the three antipodals, all haploid ($1N$), and the fused polar nuclei now in process of becoming $2N$. At this stage of development the egg is ready for fertilization (Fig. 300, *G*).

The male gametophyte, originating with the microspores as a result of meiosis in the microsporocyte, at maturity is also a greatly reduced structure (Figs. 297, 301, 306, *C*). The microspores produced as a result of the maturation processes germinate and develop to a considerable extent within the sporangium before they are shed. Development consists of nuclear divisions primarily. The microspore content divides into two parts of unequal size, usually without forming a wall. The larger of these

is known as the **tube cell** and the smaller the **generative cell**. The generative cell normally divides into two elongated cells which are the **male gametes**, or **sperms**. The male gametophyte in this condition is called the pollen grain. At about this stage the pollen grains are shed from the anthers and are transferred to the stigma of the flower. The process of transfer is called pollination. It may be effected by wind, insects, or other means. The further development of the gametophyte consists in the production of a pollen tube which penetrates the stigma and grows down through the style of the pistil. The pollen tube acts as a carrier for the male gametes, or sperms, which are formed by the division of the generative cells. The two nonmotile sperms thus formed pass down the pollen tube and are carried by the tube to the female gametophyte within the ovule. The division of the generative cell may occur either before or after the pollen grains are shed.

Fertilization, Embryo, Seed, and Seedling. As the female gametophyte is nearing maturity, conditions at the same time are also favorable for the growth of the pollen tube through the tissues. It penetrates the micropyle and passes into the cavity of the embryo sac where the contents of the pollen tube, consisting of tube nucleus and the two male gametes, are discharged. Fertilization is accomplished by the fusion of one of the male gametes with the female gamete, or egg. This results in the production of a diploid nucleus, which is the nucleus of the first cell of the new embryo. Fertilization, therefore, initiates the new sporophytic phase. A second fusion also normally takes place which involves the two polar nuclei and the second male nucleus (Fig. 306, *C*). This is termed triple fusion and results in the production usually of a triploid ($3N$) nucleus, the **primary endosperm nucleus**. The whole process, once thought to be very rare, is called **double fertilization**, because of the fertilization of the egg by one male gamete and the fusion of the second with the two polar nuclei, and is now regarded as the usual occurrence in angiosperms.

The fusion of the male and female gametes results in the production of the zygote, a diploid structure, and this process, therefore, marks the end of the gametophytic phase and the beginning of the sporophytic phase. The zygote develops into the embryo of the seed and finally, after germination, into the seedling and mature sporophyte. The triple fusion of male gamete and two polar nuclei is followed by successive divisions which result in a mass of $3N$ tissue in which a large amount of food is stored (Figs. 302; 306, *D*, *E*). In certain plants, more than three nuclei may fuse to form the endosperm tissue. It may be $5N$ or even $7N$ tissue. This tissue, called the **endosperm**, nourishes the young embryo and the seedling in the early stages of its development and at the time of the germination of the seed.

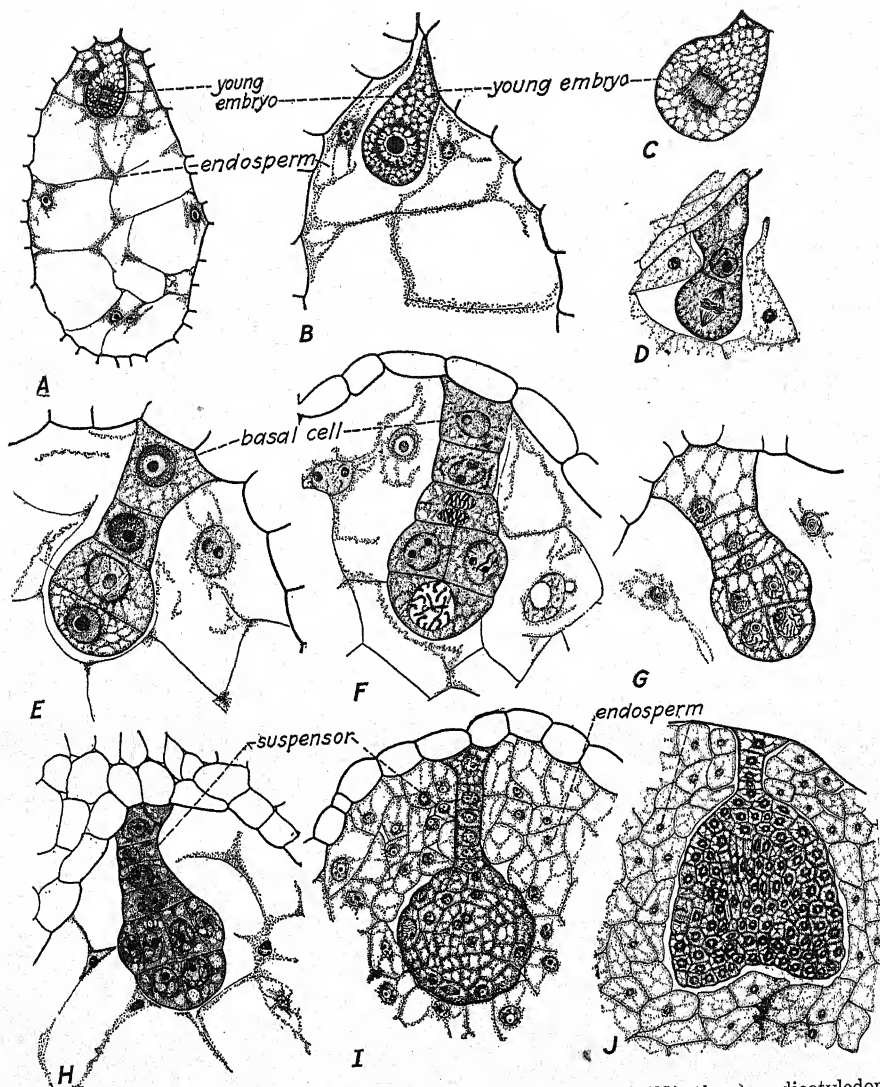


FIG. 302. Development of the embryo and endosperm in tobacco (*Nicotiana*), a dicotyledon. A, complete embryo after fertilization with the young embryo and developing endosperm; B, detail of A; C-J, stages in development of embryo and surrounding endosperm by cell multiplication and differentiation, endosperm in later stages becoming more compact; J, cotyledons beginning to be differentiated. (J drawn by Paul Sacco.)

While details of the development of the embryo vary and present considerable diversities in the several groups of angiosperms, certain features may be regarded as being fairly general. The zygote at first divides into two cells (Fig. 302, A, C). Other divisions follow and an elongated struc-

ture, consisting of four or five cells, is soon formed (Fig. 302, *E*). This structure is termed the **proembryo**. The proembryo is slender in some species and much more short and massive in others. The proembryo quite early becomes differentiated into a suspensor and an enlarged spherical terminal portion, the latter forming the embryo proper. The suspensor often remains visible until the embryo is well developed. The basal cell of the suspensor is attached to the wall of the embryo sac and is enlarged in many species of plants. Rapid growth of the embryo finally results in the production of the root portion (radicle), the stem, and the cotyledons (Figs. 112; 302, *J*; 303).

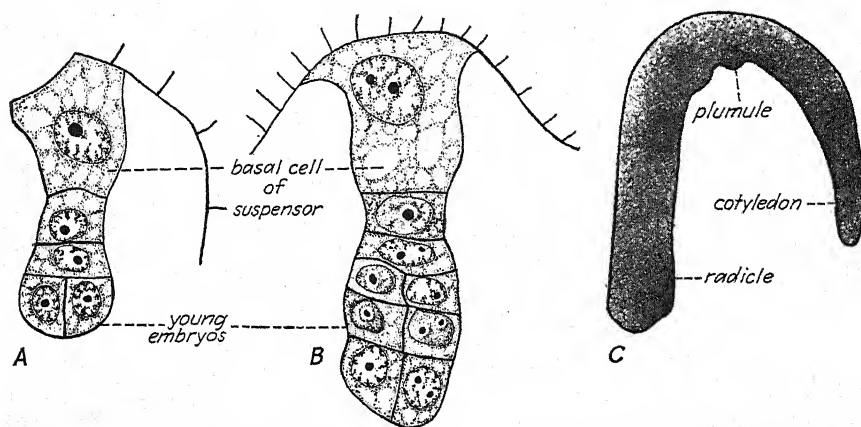


FIG. 303. Embryo development in *Sagittaria*, a monocotyledon. A and B, young stages showing basal suspensor cells and suspensors, the tip being the embryo proper; C, older embryo.

Coincident with the growth of the embryo, the endosperm develops by rapid cell division into a nutritive tissue (Figs. 302; 306, *D*, *E*). The ovule enlarges to keep pace with the rapidly growing embryo and endosperm. The integuments thicken and harden, thus developing into seed coats (Figs. 123 to 125). The seed is, therefore, a rather complex structure consisting of the embryo, the new diploid or sporophytic structure; the endosperm, a generally triploid nutritive tissue; and the various seed-coat layers which, developing from the integuments, are diploid structures but belong to the old sporophytic generation.

Variations in Reproductive Processes—The Lily. Not all angiosperms show this same development. Some, for example, certain of the orchids, produce only three cells in the megaspore row in the ovule following the maturation processes. This smaller number results from the failure of one of the nuclei of the first of the maturation divisions to continue with the second division. In other angiosperms, the embryo sac develops into a structure with many more than the typical eight nuclei.

One well-known plant, the lily, widely used as illustrative laboratory material, has long been known to be atypical in the development of its megaspores. It is now known to have other important divergences from the usual for angiosperms. The female gametophyte of the lily has been considered one of the simplest and most greatly reduced gametophytes among the angiosperms. Investigations by Cooper have shown that this feature of the life history of this widely studied plant was formerly misinterpreted. The following is an account of the most acceptable interpretation of the development of the female gametophyte within the ovule of the lily. The maturation processes in the megasporocyte of the lily result in the production of four nuclei not separated by cell walls, but floating in the common cytoplasm of the old megaspore (Figs. 304, 305). These four nuclei represent the four megaspores. One of these four nuclei remains at the micropylar end of the "embryo sac," while the other three migrate to the opposite or antipodal end of the embryo sac, and all four nuclei divide simultaneously (Fig. 305). This constitutes the third division in the developing embryo sac. The division of the three migrating nuclei in the antipodal end of the sac is accompanied by a fusion of the dividing nuclei (Fig. 305, *D*). It is this unusual feature of the fusion of nuclei while they are dividing that so long escaped observation. Many abnormal features such as multipolar spindles are described at this stage. Eventually the fusions are completed and a bipolar spindle of regular appearance is formed (Fig. 305, *E*). This spindle, as a result of the fusion of three $1N$ or haploid nuclei, has three times the number of chromosomes of the spindle in the micropylar end of the embryo sac which is that of an ordinary haploid nucleus. Following the third division—that just described—the embryo sac shows four nuclei and this is, therefore, the second four-nucleate stage. It differs in appearance from the first four-nucleate stage. In the first four-nucleate stage, the embryo sac was evenly filled with granular cytoplasm and the four nuclei were all of approximately the same size (Fig. 305, *B*). In the second four-nucleate stage, the cytoplasm contains one or more large vacuoles and the nuclei are of unequal size and of diverse appearance (Fig. 305, *F*). The two $1N$ nuclei at the micropylar end of the sac are small, and the two at the antipodal end, actually $3N$ as a result of the fusion previously noted, are large. The fourth division follows, the four nuclei dividing to form the eight-nucleate stage (Fig. 306, *A*, *B*). This division has been observed previously, but it was interpreted in all the earlier accounts as the third division. The eight-nucleate stage of the embryo sac has four $1N$ nuclei at the micropylar end and four $3N$ nuclei of unequal size at the antipodal end, the smaller two of the latter tending to disintegrate early (Fig. 306, *B*).

These eight nuclei are finally arranged as follows. One of the $1N$ nuclei from the micropylar end of the enlarged embryo sac moves now to the center of the embryo sac. It is met near the center by one of the $3N$ nuclei from the antipodal end of the sac. These are termed the polar nuclei. Upon reaching the center, they stay together and eventually fuse to form the fusion nucleus. The fusion nucleus in the lily, therefore, contains $4N$ chromosomes. Of the three $1N$ nuclei remaining in the micropylar end of the sac, one becomes the female gamete, or egg, and the other two are the synergids. At the other end of the embryo sac the three remaining $3N$ nuclei are the antipodals (Fig. 306, *B*). They are functionless. With this arrangement of nuclei, the female gametophyte is mature.

Following the entry of the pollen tube through the micropyle, double fertilization normally occurs in the lily (Fig. 306, *C*). One sperm with the haploid number of chromosomes fuses with the egg nucleus, forming a diploid zygote which develops into the embryo. The second sperm unites with the polar nuclei previously mentioned.

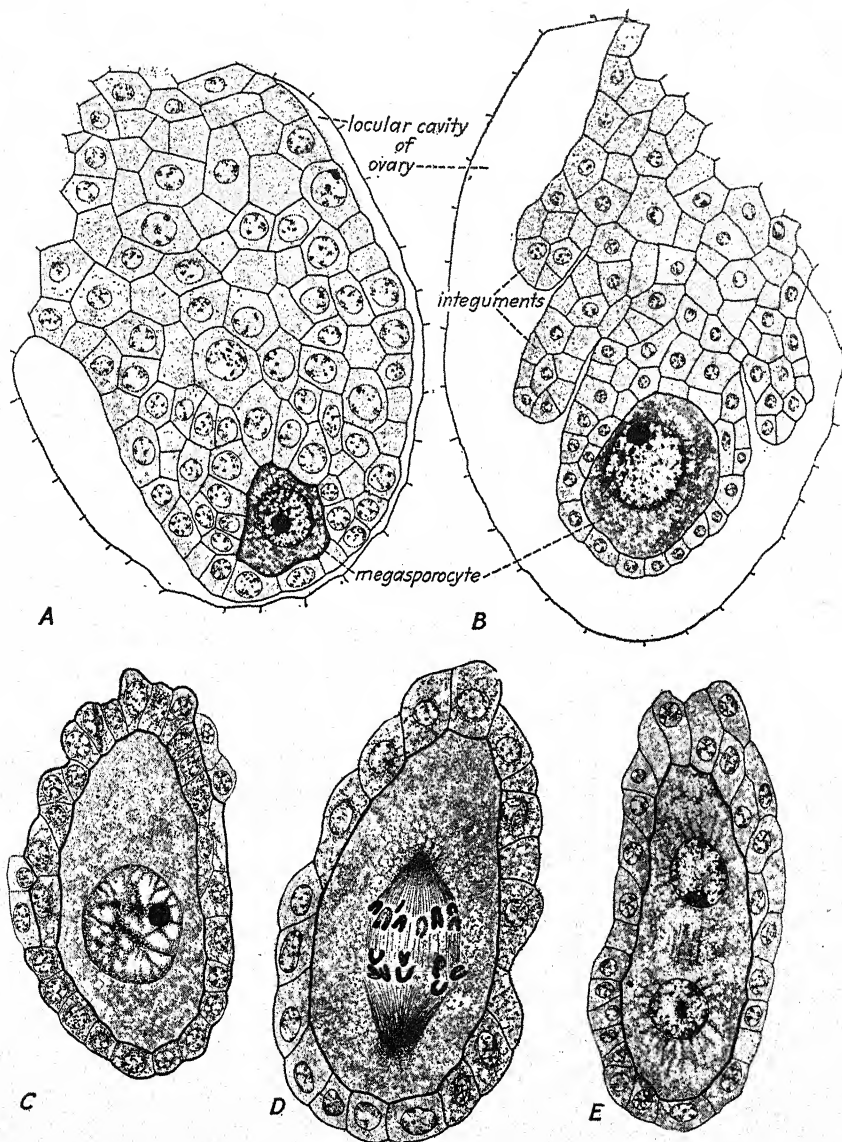


FIG. 304. The ovule and megaspore mother cell (megasporocyte) of *Lilium*. A, longitudinal section of young ovule in the locular cavity; megaspore mother cell is differentiated as a large subepidermal cell; B, slightly older ovule with integuments developing; megasporocyte increasing in size; C, megaspore mother cell enlarging; the diploid nucleus in the prophase; D, anaphase of the first maturation division in the megasporocyte; E, the two-nucleate stage of the embryo sac following the division in D.

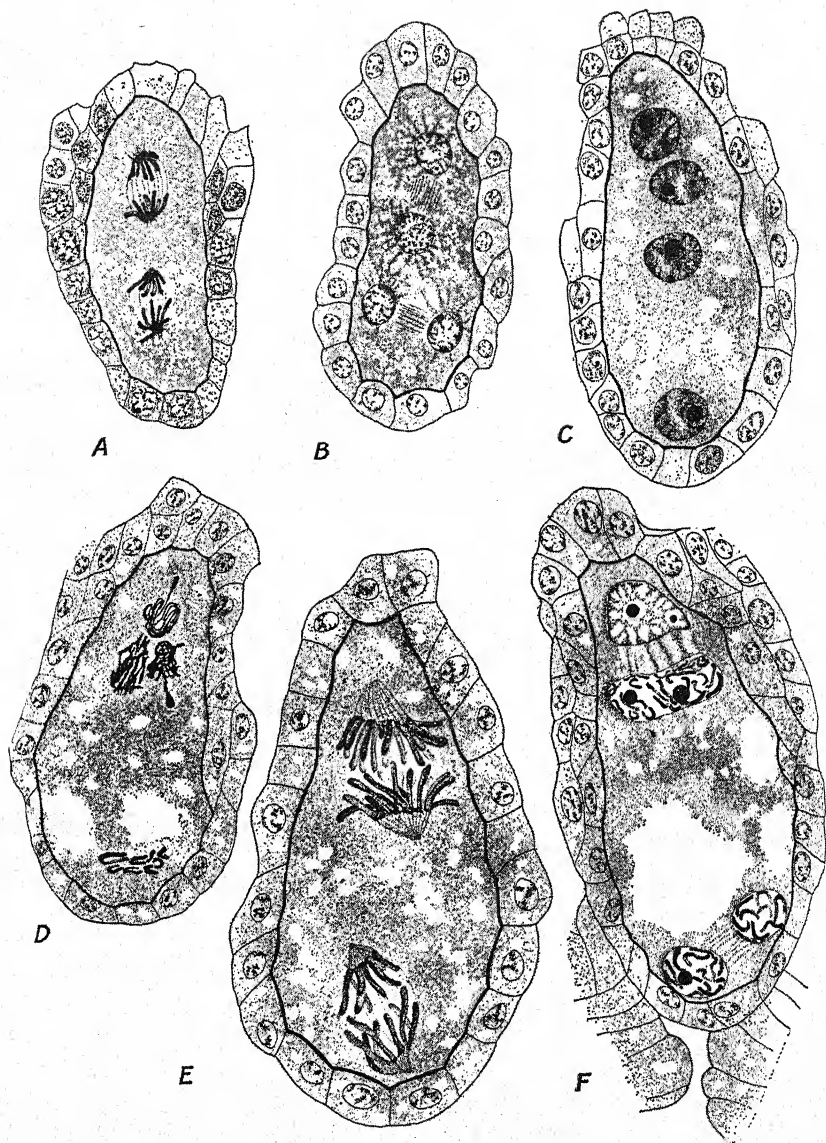


FIG. 305. Further development and behavior of the megaspores of *Lilium*. A, anaphases of the second maturation division (continuation of Fig. 304, D and E); B, the four haploid nuclei representing the four megaspores. This represents the **first four-nucleate condition**; C, three of the (megaspore) nuclei migrating to the antipodal (upper) end of the "embryo sac"; one nucleus remains at the micropylar (lower) end; D, all four nuclei in division. The spindles of the three migrants at the antipodal (upper) end are fusing to form a multipolar figure; E, a further development of the stage shown in D; the division spindle at the antipodal (upper) end of the sac is that of the triploid nucleus resulting from the fusion of the spindles similar to those shown in D. The spindle at the micropylar (lower) end is that of a haploid nucleus; the difference in chromosome number is illustrated; F, the **second four-nucleate condition** in the "embryo sac" resulting from divisions similar to those shown in E. The two nuclei at the antipodal (upper) end are triploid, while the two in the micropylar end are haploid; the difference in chromosome number is illustrated. (C, D, and F drawn from slides furnished by Dr. George H. Conant.)

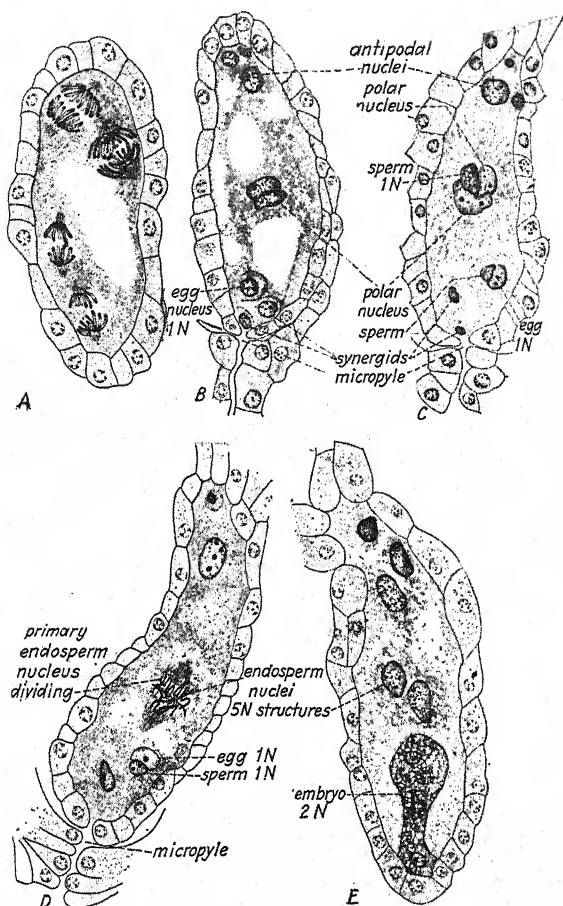


FIG. 306. Further development of the female gametophyte and fertilization in *Lilium*. A, division of the nuclei of the second four-nucleate stage shown in Fig. 305, F; the two antipodal (upper) division spindles are those of triploid nuclei and the two micropylar (lower) division spindles are those of haploid nuclei; the result of this division will be eight nuclei, four triploid nuclei in the antipodal end of the embryo sac and four haploid nuclei in the micropylar end of the sac; B, the eight-nucleate stage of the female gametophyte; the egg nucleus and two synergids, all haploid structures in the micropylar end of the embryo sac, and three small triploid nuclei in the antipodal end; one triploid nucleus and one haploid nucleus are fusing in the center; these are the polar nuclei; C, double fertilization in the lily embryo sac; one haploid sperm nucleus is fusing with the egg nucleus in the micropylar end of the embryo sac. The second haploid sperm nucleus is fusing with the two polar nuclei; the sperm is haploid, one polar nucleus is haploid, and the other is triploid. Thus the endosperm nucleus resulting from the fusion of the three nuclei is a pentaploid (5N) structure; three small, antipodal nuclei remain in the upper end of the sac; D, fertilization and division of the endosperm nucleus; the sperm and egg are uniting in the micropylar (lower) end of the embryo sac, while the primary pentaploid (5N) endosperm nucleus is dividing in the central region; E, development of the young embryo and the endosperm; the diploid embryo is located in the micropylar (lower) end of the embryo sac, while several pentaploid endosperm nuclei resulting from successive divisions of the endosperm nucleus occupy the central and antipodal parts of the sac. (B-E drawn from slides furnished by Dr. George H. Conant.)

This fusion results in a $5N$ condition in the **primary endosperm nucleus**. Following these fusions the zygote develops into the young embryo and the endosperm nucleus begins division to form the endosperm tissue (Fig. 306, *D*). Sometimes the development of the embryo and endosperm begins together, while at other times one or the other precedes.

Summary of the Angiosperms. The angiosperms, a vast group of plants, may be characterized as showing many morphological, anatomical, and reproductive diversities. Certain features are common to all members of the group. Ovules and seeds are borne enclosed in an ovary formed by the fusion of the megasporophylls or carpels. This structure ripens into some sort of pod or fruit and is the feature which distinguishes the angiosperms from the other group of seed-bearing plants, the gymnosperms. The presence of vessels made up of a vertical series of cells is an important anatomical feature. The life history in the group is characterized by a very highly developed sporophytic, or diploid, structure and greatly reduced male and female gametophytes, or haploid structures. In a corresponding manner the sporophytic phase is lengthened and the gametophytic phase is shortened.

The maturation processes take place regularly in the anthers and in the ovules, resulting in the production of haploid structures, the microspores and megaspores, respectively. Each microspore grows into a pollen grain which eventually produces a pollen tube and two sperms. The megaspores never escape from the ovule in which they are produced. The term embryo sac is applied to the female gametophyte. This structure generally consists of eight nuclei held in the common cytoplasm of the sac. These nuclei are haploid and represent all that there is of the female gametophyte. At maturity the female gametophyte consists of an egg, two synergids, two polar nuclei, and three antipodal nuclei.

At fertilization, the two nonmotile sperms are carried to the embryo sac in the pollen tube. The sperms are freed from the pollen tube when its membrane bursts. One sperm fuses with the egg, forming the diploid zygote which grows into the embryo. The second sperm fuses with the two polar nuclei, usually forming a triploid ($3N$) nucleus which by divisions and wall formation develops the endosperm. The integuments of the ovule form the coats of the seed. The germination of the seed and the growth of the seedling into a mature sporophyte complete the life cycle.

Origin of the Angiosperms. Investigations of the fossil remains of plants indicate that the flowering plants first appeared in the Jurassic period of the Mesozoic age and gradually became more prominent during the Cretaceous period. At present, they constitute the dominant features of the flora of the earth. Although the time of the development of the flowering plants may be read in the fossil records, the methods by which they originated and their relationships are not clear. The general student may be unable to solve the intricate problem of the origin and relationships of the angio-

sperms, but he should be appreciative of the problem and the evidence which enters into its solution. Among the features considered in the effort to determine the origin and evolution of the angiosperms are the development of flowers, the production of seed, and the development of closed carpels. Seed production, common to both angiosperms and gymnosperms, apparently first appeared in the Carboniferous period of the Paleozoic age. The origin of the flower, veiled in antiquity, is a problem difficult of solution. A brief review of certain structural features of primitive and advanced plants may be helpful in providing a background for this problem. It should be emphasized, however, that the plants mentioned below are only distantly related and do not form a phylogenetic line.

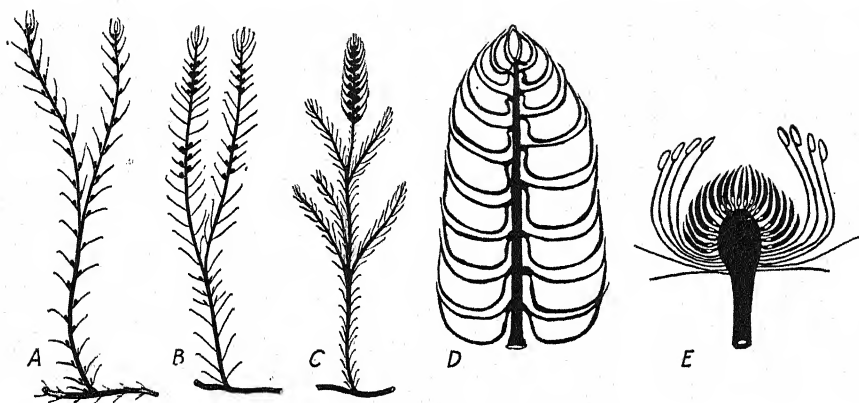


FIG. 307. Strobili, cones, and flowers. A, extremely primitive type of strobilus, every leaf a sporophyll bearing sporangia as represented in *Lycopodium pithyoides*; B, strobilus type, with leafy sporophylls composing the fertile regions alternating with the purely vegetative regions of the stem bearing the unmodified leaves as illustrated by *Lycopodium Selago* and *L. lucidulum*; C, cone with sporophylls reduced and sharply differentiated from the vegetative leaves as represented by *L. obscurum*; sporophylls and sporangia all alike and not very leafy; D, extreme type of cone; longitudinal section of staminate cone of the conifers. Sporophylls much reduced and sporangia all of one kind with leafy features entirely eliminated. The compact nature is a cone characteristic; E, primitive flower type with both mega- and micro-sporophylls present in the same general structure. (All diagrammatic.)

A consideration and review of the structure and possible relationship of strobili, cones, and flowers may be helpful as a background in seeking a solution of the origin of the flowering plants. It is well in this discussion to keep in mind that there are both the extremely popular and the scientific uses of the terms cones and flowers.

The term strobilus may be considered as applicable to the most primitive of the structures of the series strobilus, cone, and flower. In general, the strobilus may be regarded as the more leafy type of structure. Certain species of the genus *Lycopodium* are good examples of the strobilus. *Lycopodium pithyoides*, a species native of southern regions, bears sporangia in the axil of every leaf (Fig. 307). These may be considered as illustrating the beginnings of strobili. *Lycopodium lucidulum*, common in the North Atlantic states, and *Lycopodium Selago* represent a development toward a strobilus restricted to a definite region. In *Lycopodium lucidulum* the slightly modified sporophylls occupy a definite zone on the stem (Figs. 252; 307, B). These

fertile zones alternate with zones producing only vegetative leaves. The sporophylls are smaller than the vegetative leaves in *Lycopodium lucidulum* but very leaf-like. Other species of *Lycopodium* (*Lycopodium obscurum* and *Lycopodium complanatum*) have the sporophylls very much reduced in size and quite unlike the vegetative leaves. The sporophylls in these species are aggregated into definite terminal structures (Figs. 252; 307, *C*). Only one kind of sporangium bearing one kind of spore is produced in these cases. The term cone may, therefore, be applied to these structures. In the staminate cones of the conifers, the sporophylls are reduced, not leaf-like, and only one kind of spore is produced. The structure is decidedly not leafy. These structures may be regarded as excellent examples of true cones (Figs. 272, *A*, 307, *D*). The ovulate "cones" of the conifers, long a subject of investigation and controversy, are not simple structures as are the staminate cones but extremely complex. They may perhaps be properly regarded as inflorescences.

Flowers may be regarded as bisexual structures; *i.e.*, they bear both ovulate and staminate sporophylls (Figs. 105; 295; 307, *E*; 308). Modern thought on the subject of the origin of the flower tends more and more in the light of fossil study to seek the origin of flowers early in geological history. Possibly the flowering plants may be regarded as originating independently of the main gymnosperm lines. Their remote ancestors may have been the early seed-bearing ferns, or pteridosperms. Shortening of the stem axis and fusions of the parts of these seed-fern structures would result ultimately in the development of structures similar to the flower.

It is possible that structural development along similar lines may have occurred in the evolution of the angiospermous flower. Among the most ancient and most primitive flowering plants are the magnolias, of the family Magnoliaceae, the buttercups, of the family Ranunculaceae, and the water lilies, of the family Nymphaeaceae. The diagram at *E* in Fig. 307 shows a conventionalized illustration of the flower in these primitive types. In this connection it is of interest that Arnold¹ in his recent book on paleobotany states that the oldest fossil angiosperms known with certainty are water lilies.

In consideration of the origin of angiosperms, certain possibilities are open. *One possibility* is the older suggestion that the angiosperms, a modern group, originated as a branch from some of the higher gymnosperms. The high specialization of most of the gymnosperms is, however, considered as evidence opposed to this hypothesis. *Another possibility* would derive the angiosperms from the lower gymnosperms, the ancient seed bearing fern-like plants, the Cycadofilicales or pteridosperms. *A third possibility* might be the separate evolution of the angiosperms from the ancient paleozoic fern plexus. This would necessitate the assumption of a separate origin of the seed habit distinct from that occurring in the gymnosperms. This assumption is not necessarily untenable since heterospory, fundamental to seed production, is known to have been developed in paleozoic ferns. *A fourth possibility* is that the flowering plants may have developed as a distinct branch from the most ancient and primitive vascular plants, the Psilopsida. Because of the presence of leaf gaps, in the vascular cylinder, the angiosperms are associated with the Pteropsida, or fern-like plants. This feature suggests relationship with either the ancient ferns or with the pteridosperms.

¹ C. A. Arnold, "An Introduction to Paleobotany," McGraw-Hill Book Company, Inc., New York, 1947.

CHAPTER 19

FAMILIES OF ANGIOSPERMS

The angiosperms constitute the dominant vegetation of the earth today. Their great economic importance and the general interest manifested in flowering plants generally probably justify at least a brief consideration of some of the more important families into which the group has been divided.

Primitive and Advanced Floral Structure. As stated previously, the angiosperms are divided into two groups, the dicotyledons and the monocotyledons. Within these two main subdivisions, the orders and families are usually arranged according to their possible evolutionary positions, based mostly on flower characteristics. The earliest flowers are thought to have resembled a cone, or strobilus, which consisted of an elongated axis with a large and indefinite number of spirally arranged and separate stamens (microsporophylls) and pistils (megasporophylls). Since the buttercups (Ranunculaceae) and the magnolias (Magnoliaceae) (Fig. 308) have many of these characteristics, they are thought to represent this primitive type best. Advances in floral evolution are indicated by the following:

1. *A Whorled or Cyclic Arrangement of the Parts of the Flower.* The floral axis in flowers of this type is greatly shortened, and the parts appear in whorls or circles. In the common buttercup, the sepals and petals are usually cyclic but the stamens and pistils often have the more primitive spiral arrangement (Fig. 309, B-D).

2. *A Reduced and Definite Number of Floral Parts.* In the more primitive types of flowers there are usually large and indefinite numbers of flower parts (Figs. 308; 309, B-D). More advanced types have fewer and definite numbers of stamens, pistils, petals, and sepals (Figs. 311, B; 313, F; 318, A). In the higher members of the dicotyledons, the number of each of these parts is often two or five or multiples of these, while in the monocotyledons the number is usually three or multiples of three. The more advanced flowers also have fewer whorls or cycles of organs. Thus in many members of the heath family there are five whorls, consisting of one whorl or circle each of sepals, petals, and pistils (carpels) and two whorls of stamens. In the phloxes and morning-glories there are only four whorls of organs, a condition resulting from the presence of only one whorl of stamens.

3. *Differentiation of the Perianth.* The differentiation of the perianth into calyx and corolla probably occurred very early in the evolution of the flower. Today, this condition of the perianth is found in what are considered primitive types of flowers (e.g. Ranunculaceae), as well as in many of the higher forms (most of the families of dicotyledons). In the lilies and in other monocotyledons, there is often little difference between sepals and petals (Fig. 323, A), both being showy and often highly colored. This condition is considered by some as more advanced than the one in which the calyx is green and the corolla more differentiated and showy (Fig. 313, F). In some flowers, the perianth is absent altogether, a condition thought to have been derived by reduction from a flower having a perianth.



FIG. 308. The relatively primitive flower of the tulip poplar (*Liriodendron tulipifera*), a member of the family Magnoliaceae, showing the numerous separate pistils spirally arranged on the elongated floral axis, and the numerous stamens of indefinite number. The three sepals and six petals have a cyclic arrangement.

4. *Coalescence and Adnation of Floral Parts.* All the floral organs of primitive flowers are entirely separate from each other (Figs. 308; 309, B, C). In more advanced forms, members of the same cycle are united or coalesced. Thus the sepals may be united into a calyx tube with only their tips separate, as in the potato family (Fig. 311, G). The petals also may form a tube, as in the potato, the mints (Fig. 313, F), and morning-glories. On the basis of coalescence of perianth parts, the dicotyledons are sometimes subdivided into two main groups, the **Archichlamydeae** or **Choripetalae**, in which the individual members of the calyx and corolla are entirely separate from each other or the perianth as a whole is poorly developed, and the **Metachlamydeae** or **Sympetalae**, in which the petals are united into a gamopetalous corolla. The stamens also may be united into a complete cylinder by their filaments alone, by their anthers alone, or by both. This occurs in the potato family (Fig. 311, B, C). The carpels are often coalesced to form a compound pistil, as in many families of the angiosperms.

Adnation, or the fusion of members of different cycles, also occurs in the more advanced types of flowers. Thus the floral tube may be united with the ovary, as in the carrot and other higher families (Fig. 316, *C*). The stamens may appear to be borne on the corolla, as in mints, figworts, and composites (Fig. 318, *F*), and the corolla may appear to be borne on the floral tube at the top of the ovary (Figs. 314, *A, C*; 316, *B, I*).

5. *Perigyny or Epigyny as Opposed to Hypogyny*. The term **hypogyny** (literally, under the ovary) refers to the condition in which sepals, petals, and stamens are attached to the receptacle at the base of, and entirely free from, the ovary (Fig. 310, *B*). The ovary, in this case, is said to be **superior**. This condition is considered relatively primitive. It is found in buttercups, pinks, mustards, and legumes. Flowers in which the basal parts of the calyx, corolla, and stamens are united into a floral tube which surrounds, but is free from, the ovary are known as **perigynous** flowers, the term "perigyny" meaning "around the ovary." In such flowers, the petals and stamens appear to be borne on the upper rim of the floral tube which is sometimes incorrectly called a calyx tube. The ovary itself is superior. This condition is found in some members of the rose family (Fig. 314, *C*) and is usually considered more advanced than hypogyny. The most advanced condition in the position of the ovary with respect to the other floral parts involves the fusion of the floral tube to the ovary wall in such a manner that the ovary appears to be situated below the remaining floral organs. This condition is known as **epigyny**, a term meaning "on or above the ovary." The ovary is said to be **inferior**. Members of the orchid family, the carrot family, and the sunflower family (Fig. 318, *A, F*) have epigynous flowers.

6. *Irregularity or Bilateral Symmetry as Opposed to Regularity or Radial Symmetry*. The primitive buttercup type of flower has a radial symmetry, *i.e.*, it is uniformly developed on all sides of the central axis, so that it may be divided through the center in any direction to give two like halves. Irregularity of flowers results from an unequal development on one or more sides of this central axis. In some flowers, only the calyx or the corolla is irregular (Fig. 313, *B*). The two-lipped flowers of the mints and the butterfly-like flowers of legumes (Figs. 313, *B*; 315, *F, H*) are distinctly bilaterally symmetrical; *i.e.*, they can be cut in only one plane to give two like halves. Bilateral symmetry in flowers is often correlated with a high degree of specialization in insect pollination.

In many of the families of angiosperms, the flowers may be quite advanced in some respects but primitive in others. Thus the mints have all the advanced features mentioned except that the flowers are hypogynous; the orchids, usually considered among the most advanced monocotyledons, have the relatively primitive feature of separate petals. Many other combinations of advanced and primitive characteristics occur, making it

sometimes difficult properly to place a group. In addition, some groups of angiosperms formerly thought to be primitive and ancient are now considered to have been reduced from types with many floral parts. Among these are the so-called "Amentiferae" (ament or catkin bearers), including the beeches, oaks, chestnuts, hickories, walnuts, birches, willows, poplars, and alders. The cattails and grasses, in the monocotyledonous group, are also thought to have reduced flowers. A detailed discussion of the possible lines of development in floral evolution in the angiosperms is beyond the scope of the present book. In the pages that follow, attention is given to the size, distribution, economic importance, and general morphological characteristics of a few representative families of dicotyledons and monocotyledons.

FAMILIES OF DICOTYLEDONS

Family Ranunculaceae (Buttercup Family). This family (Fig. 309), named for the genus *Ranunculus*, the well-known buttercup group, includes about 1,200 species widely distributed in the north temperate and north frigid zones. In addition to the buttercups, the anemones, hepaticas, and marsh marigolds are common members of our native flora. Columbines, peonies, larkspurs, and *Clematis* are familiar as ornamental plants. A few species are sources of drugs, for example, *Aconitum* and *Hydrastis*. Many, if not all, of the western larkspurs are poisonous to cattle.

Most members of the family are herbaceous, but a few species like *Clematis* are woody. The leaves are typically palmately veined and palmately lobed, although unlobed simple leaves and compound leaves are found within the group. In most cases, the phyllotaxy is spiral. Stipules are seldom present.

The flowers are usually conspicuous, often solitary and terminal, but sometimes in loose or compact racemes or in panicles. In most cases, they are perfect, but imperfect flowers occur. Most species have regular flowers, but larkspurs and related forms have irregular flowers. The flowers are hypogynous.

In some species, the perianth is represented only by a calyx, which, in some cases, is colored and resembles a corolla. In other forms, both calyx and corolla are present. The number of petals is commonly not constant for a given species, and it may be as great as 12 or 15 in single flowers.

The stamens are usually numerous (Fig. 309, C) and are sometimes spirally arranged, but occasionally are only five in number and are reduced in arrangement to a single cycle. The pistils are simple and are usually numerous and spirally arranged over a globose, conic, or elongate re-

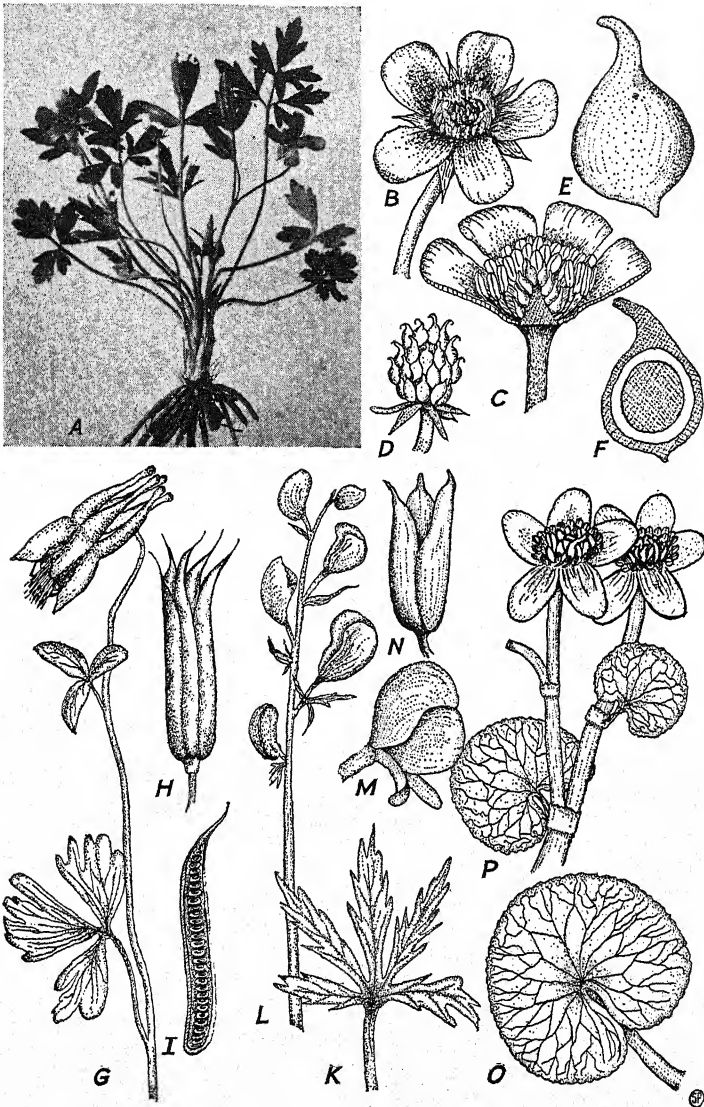


FIG. 309. The buttercup family (Ranunculaceae). *A*, a common woods buttercup, showing leaves, stem, roots, and flowers; *B*, a single flower enlarged, showing many centrally placed simple pistils, many stamens, five petals, and five sepals; *C*, lateral view of vertical section of flower, showing arrangement of pistils on the conic receptacle; *D*, the matured pistils after disappearance of stamens and corolla; *E*, a single mature pistil; *F*, section through a single pistil, showing the single ovule; *G-I*, columbine; *G*, flowering stem, showing the five elongated calyx spurs; corolla not visible; *H*, the mature fruits; *I*, longitudinal section of a single fruit; *K-N*, monkshood; *K*, a single leaf; *L*, the flower stalk; *M*, a single flower, the exposed parts being the colored sepals of the irregular flower; *N*, fruits; *O-P*, marsh marigold; *O*, leaf; *P*, flowering stalk; floral structure as in the buttercup. (Drawings by Edna S. Fox.)

ceptacle (Fig. 309, *C*). Each one is entirely separate from all the others. Occasionally, the pistils are reduced in number, even to one in some species. In a few cases, there is a slight union of carpels. The fruit is commonly a follicle or an achene, but in the baneberry (*Actaea*) and a few other species it is a berry.

In summary, the outstanding morphological features shown by the majority of the flowers belonging to this family are the radially symmetrical, perfect type of flower, the numerous floral organs, indefinite in number, the spiral arrangement of numerous separate stamens and simple pistils, and the absence of cohesions or adhesions among any of the floral organs. These features all mark the group as a primitive one. The number of exceptions given to the foregoing characterization of the family are indicative of the wide variations which exist within the family. Constancy is the exception rather than the rule. This is the condition which one might expect to find in a family exhibiting primitive features which are thought to have been the starting point for the lines of development exhibited by the angiosperms.

Family Cruciferae (Mustard Family). The name Cruciferae (Fig. 310) is derived from the fact that the arrangement of the four petals of the flowers of these plants resembles a cross. This large family of about 200 genera and 2,000 species is widely distributed in the temperate and frigid zones. Many species such as the wild mustards, shepherd's-purse, and certain cresses are troublesome weeds. The candytuft, wallflower, alyssum, dame's violet, and stocks are familiar as garden plants. Rape is important as a green forage crop. Many species are avoided by grazing animals because of the acrid juice of the plants. None, however, is known to be poisonous. Economically the greatest importance of the Cruciferae lies in their use by man as food. Leaves, stems, roots, or flowers are used, as exemplified by water cress, cabbage, Brussels sprouts, radishes, turnips, kohlrabi, and cauliflower. From certain species, condiments and spices are prepared. The use of the grated root of the horse-radish is well known.

- Mustard is obtained from the seeds of black and of white mustard plants.

Most species of the family are herbaceous. Some are biennial, forming a compact rosette of leaves close to the ground the first year and sending up flowering shoots the second year. The leaves are most often simple, but are sometimes pinnately lobed and even pinnately compound. Stipules are usually absent. The phyllotaxy is characteristically spiral.

The flowers are commonly borne in racemes. Yellow is the predominating color, but white, blue, and orange flowers also occur. The presence of four petals and four sepals, with six stamens, of which four are longer than the other two, is usually sufficient to identify a plant as a member of the mustard family (Fig. 310, *B*). The arrangement of the floral organs is entirely cyclic, the flowers are hypogynous, regular, perfect, and, with

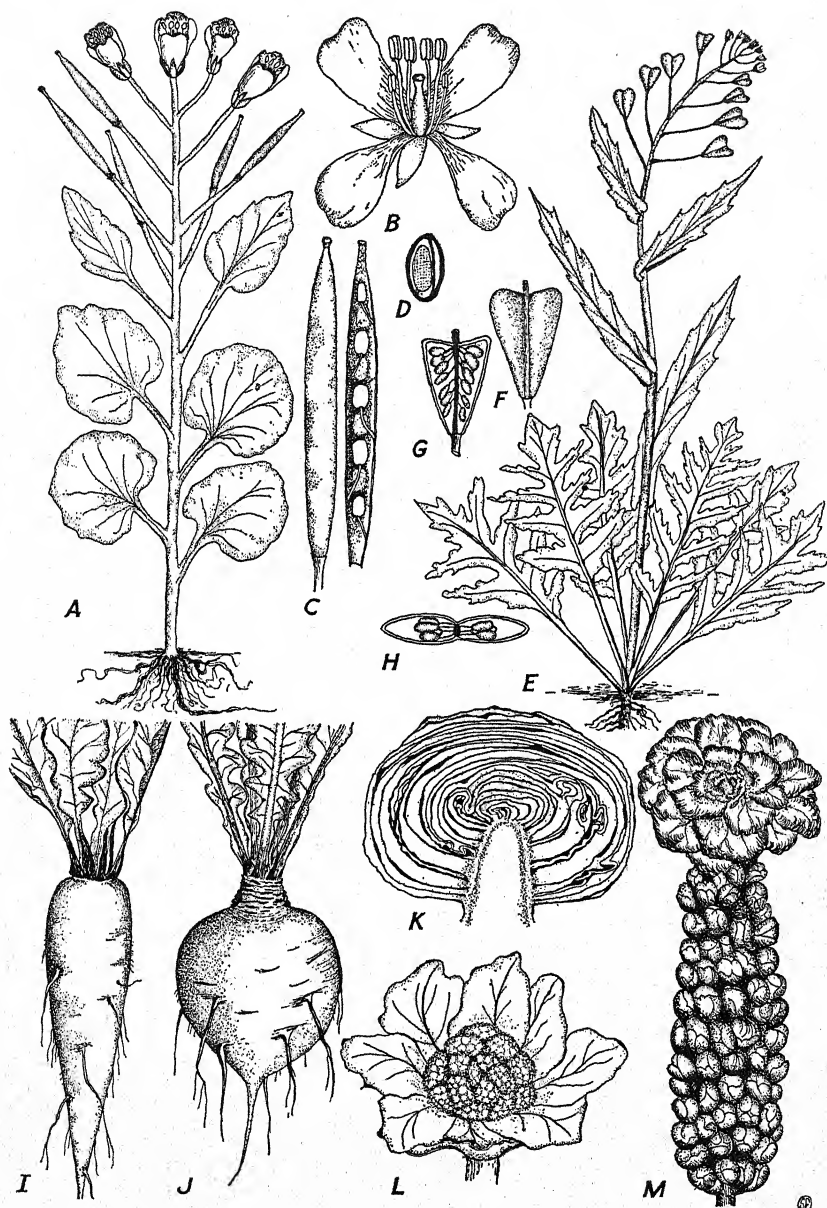


FIG. 310. The mustard family (Cruciferae). *A-D, Cardamine*; *A*, entire plant with flower and fruit; *B*, a single hypogynous and complete flower; *C*, fruits, one split lengthwise to show the seeds; *D*, cross section of the ovary; *E-H, shepherd's-purse*; *E*, entire plant with flower and fruit; *F*, a single ripened ovary; *G*, ovary cut parallel to its flattened faces, showing arrangement of ovules; *H*, ovary cut crosswise; *I*, fleshy taproot of radish; *J*, fleshy taproot of turnip; *K*, vertical section of cabbage head, a large bud; *L*, head of cauliflower; *M*, Brussels sprouts, the edible portions being the many large buds that grow on the lower part of the stem. (Drawings by Edna S. Fox.)

few exceptions, complete. The base of each petal is contracted into a narrow claw; the tip is expanded and spreading, the four tips, together, forming the cross. The four longer stamens are opposite (in front of) the petals. The pistil is compound, consisting of two carpels. Internally, the ovary is divided by a thin partition into two compartments, each one containing, usually, several to many ovules.

The fruit, like the flower, is peculiar to the mustard family and will identify the plants in a more advanced stage of development. Although it varies widely in form in the different genera and is an important character in distinguishing one genus from another, it is always a peculiar type of capsule, known as a silique or a silicle, which differs from other capsules in the presence of a thin partition stretched across the capsules between the two parietal placentae and in its method of dehiscence. The silique, characteristic of radish, mustard, turnip, cabbage, and related forms, is several times longer than broad (Fig. 310, *C*); the silicle (Fig. 310, *G*), characteristic of horse-radish, peppergrass, and shepherd's-purse, is about as broad as it is long, is thin, and is flattened on two opposite faces.

The attainment in the Cruciferae of a completely cyclic arrangement of floral organs, the reduction in their number, especially of stamens and pistils, and the compound pistil composed of two carpels represent more highly advanced features than occur in the Ranunculaceae. The hypogynous nature of the flower and the lack of coalescence, aside from the united carpels, are primitive features.

Family Solanaceae (Potato Family). The family name Solanaceae (Fig. 311) is taken from the genus name *Solanum*, which includes the potato and its relatives and the nightshades. It is a fairly large family, containing approximately 1,800 species in about 85 genera. Most of the species are tropical or subtropical in distribution, but a number occur in temperate regions. Important economic species in the group are the potato, the tomato, eggplants, peppers, and tobacco. Petunias, the bittersweet nightshade, the matrimony vine, and others are used as ornamentals. The Jimson weed, buffalo bur, horse nettle, and sometimes the ground cherry and the nightshades are often troublesome weeds. Many of the species yield poisonous or narcotic alkaloids. The drugs solanine, capsicum, belladonna, nicotine, and atropine are obtained from different species.

The plants of this family are mostly herbaceous annuals, although in the tropics some reach the stature of small trees. The leaves are spirally arranged. In some species they are simple and in others pinnately compound. Stipules are not present. The flowers are usually large and conspicuous, regular, hypogynous, perfect, and complete. The calyx is five-parted, the sepals being united below into a calyx tube. The same

condition prevails in the corolla, in which the tube is often well developed. There are five separate stamens borne on the corolla. The pistil is compound and composed of two carpels. The ovary is superior. The rel-

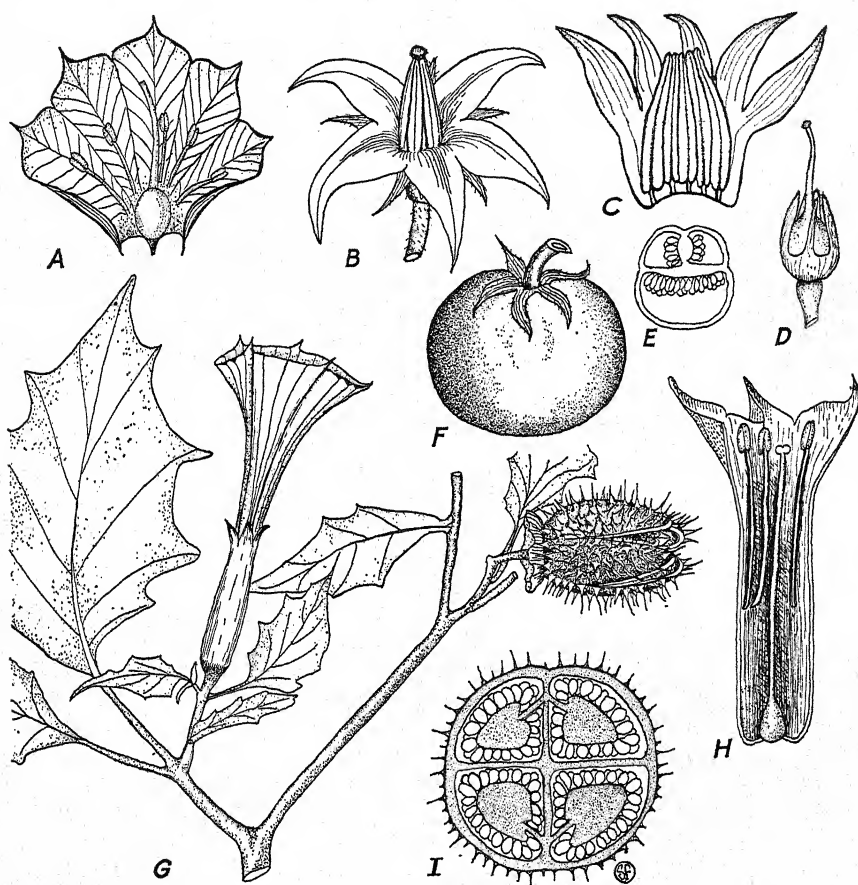


FIG. 311. The potato family (Solanaceae). *A*, flower of a ground cherry, with corolla split open to show structure; *B-F*, tomato flower and fruit; *B*, single flower, showing the stamens cohering around the pistil with stigma projecting; *C*, corolla removed and split longitudinally to show attachment of stamens; *D*, calyx and pistil after removal of corolla and stamens; *E*, cross section of ovary, showing three locules (two locules is the more common condition) and attachment of ovules; *F*, maturing fruit of tomato; *G-I*, Jimson weed; *G*, leaf, flower, and fruit; *H*, flower removed and split vertically to show relation of parts; *I*, cross section of maturing capsule, showing locules and attachment of ovules. (Drawings by Edna S. Fox.)

atively long style is terminated by a single, entire stigma. The fruit ripens into a berry, often of considerable size, as in the potato, the tomato, and the eggplant, or into a capsule as in tobacco and in the Jimson weed.

The coalescence of sepals and of petals to form, respectively, the calyx tube and corolla tube, the insertion of the stamens on the corolla, and the reduced number (two) of carpels, all point to a rather high rank, and yet the flowers are hypogynous and regular.

Family Scrophulariaceae (Figwort Family). The family (Fig. 312) named for the genus *Scrophularia* embraces about 205 genera and 2,600 species and reaches its best development in temperate regions. Common forms of our native flora are the mullein, toadflax, figwort, beardtongue, speedwell, lousewort, and painted cup. Ornamental plants include the foxgloves, snapdragons, and the empress tree. Medicinal drugs are obtained from the foxglove (*Digitalis*), mullein, and speedwell. The family contains no plants which are important as a source of food for man.

Most species are herbaceous, but a few are shrubs or trees. Annuals, biennials, and perennials occur within the family. A number of genera embrace species which are at least partially parasitic on the roots of other plants. The vegetative characters are not constant enough within the group to serve as easy means of identification.

The flowers, commonly borne in racemes, are usually more or less irregular in symmetry, those of the snapdragons and related forms having two-lipped corollas. Sepals and petals are either four or five in number and coalesced to form calyx tubes and corolla tubes, respectively. There are two, four, or five stamens, often four in pairs of unequal length (didynamous), inserted on the corolla tube, the fifth stamen represented by a staminode (sterile stamen) or absent. The superior, compound pistil consists of two carpels. The fruit is a capsule. All the floral characters except the nature of the ovary and fruit are somewhat similar to those of the mint family.

Family Labiatae (Mint Family). The name Labiatae is from the Latin noun *labium* (lip) and refers to the irregular, two-lipped corolla characteristic of flowers belonging to the mint family (Fig. 313). The Labiatae, including 170 genera and 3,000 species, are widely distributed in temperate regions, and, because they are easily recognized, the family is one of the oldest known. Pennyroyal, catnip, motherwort, horsemint, mountain mint, spearmint, and peppermint, heal-all, bugleweed, and dead nettle are common forms found along roadsides and in waste places or as weeds. Some species are extremely xerophytic. *Salvia* and *Coleus* are common ornamental plants, and catnip a common drug plant. No important food plants are found among the mints, but flavorings are obtained from many, including spearmint, peppermint, thyme, sage, and sweet marjoram.

Members of the mint family, mostly herbaceous, are easily recognized by the four-sided (square in cross section) stem bearing simple, opposite leaves which lack stipules and the irregular flower with a two-lipped

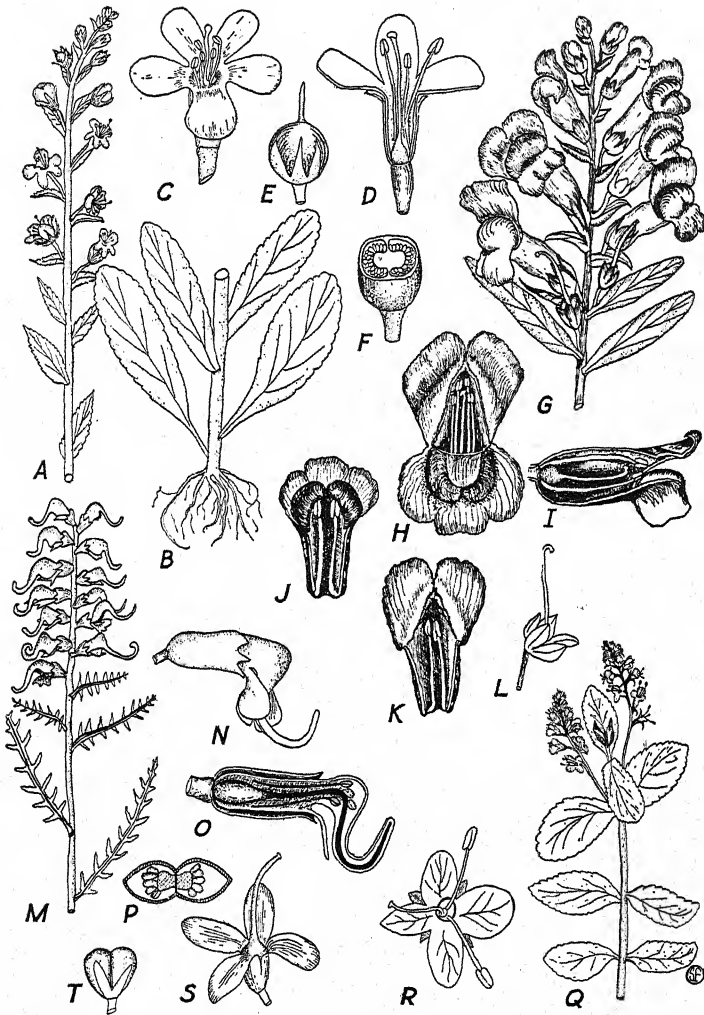


FIG. 312. The figwort family (Scrophulariaceae). A-F, moth mullein (*Verbascum blattaria*). A, upper 6 in. of plant, showing racemose inflorescence and reduced leaves; B, lower part of same plant as A; C, a single flower, showing stamens, pistil, and the slightly irregular corolla; D, single flower split vertically, showing arrangement of parts; E, fruit; F, fruit in cross section; G-L, the snapdragon (*Antirrhinum majus*); G, racemose inflorescence and the irregular flowers; H, front view of flower with the two unequal lips of the corolla opened, showing four stamens and single style; I, view of longitudinal section of flower, showing arrangement of parts; J, lower lip of corolla drawn separately; K, upper lip of corolla drawn separately; L, flower with corolla and stamens removed, showing irregular calyx and style; M-P, little red elephant (*Elephantella groenlandica*); M, upper part of plant showing spicate inflorescence and the peculiarly shaped flowers; N, a single flower with upper petal projected into a filiform beak that encloses style and stigma; O, longitudinal section of flower, with style and stigma enclosed in the beak and shown in solid black; P, cross section of ovary; Q-T, common speedwell (*Veronica officinalis*); Q, upper part of plant, showing racemose inflorescence and leaves; R, single flower, front view, showing irregular corolla, two spreading stamens, and curved style; S, flower with corolla removed, showing pistil and irregular calyx; T, ripened ovary in surface view. (Drawings by Edna S. Fox.)

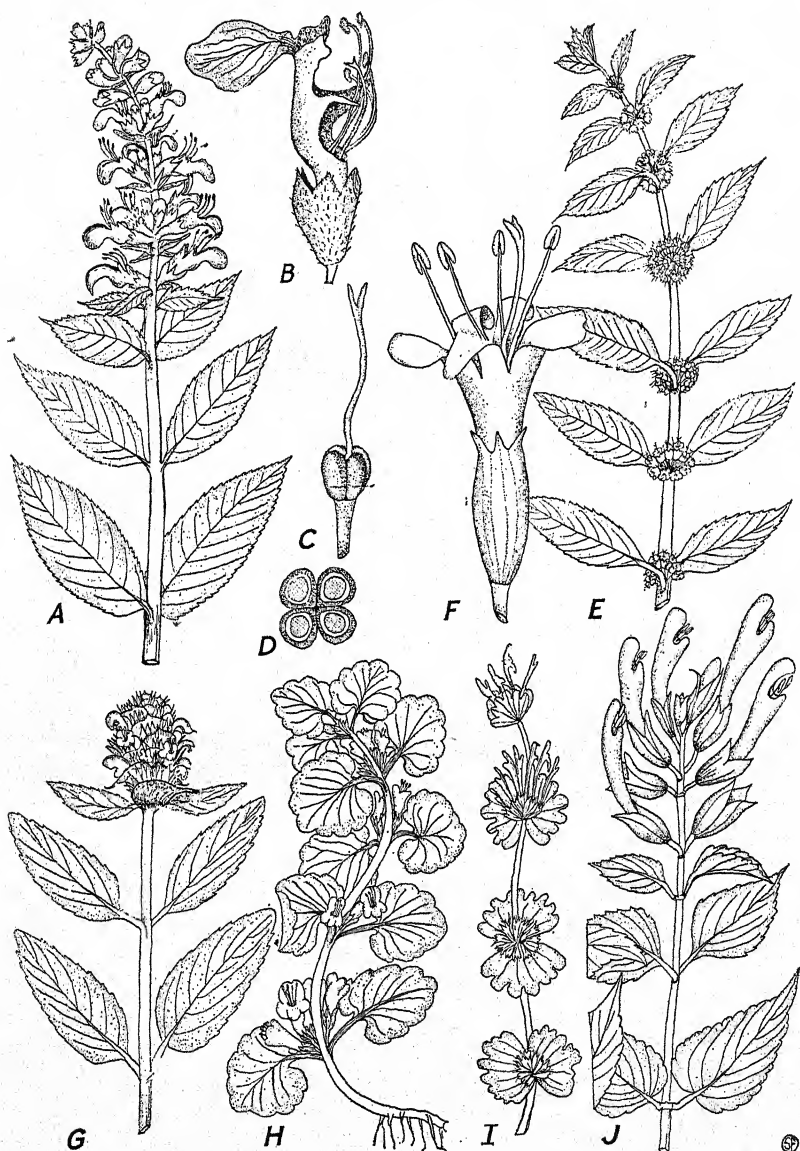


FIG. 313. The mint family (Labiatae). A-D, wood sage (*Teucrium canadense*); A, upper portion of plant with leaves and spicate inflorescence; B, a single irregular flower with four stamens and a single two-lobed style; C, gynoecium, after removal of calyx, corolla, and stamens; note the four-lobed ovary; D, cross section of the ovary, showing single ovule in each lobe; E-F, wild mint (*Mentha canadensis*); E, upper part of plant bearing leaves and flowers in axillary clusters; F, single flower only slightly irregular; G, heal-all (*Prunella vulgaris*), upper part of plant bearing leaves and a close head of flowers; H, ground ivy (*Nepeta hederacea*), a creeping mint with flowers in loose axillary clusters; I, dead nettle (*Lamium amplexicaule*), a low semitrailing mint with axillary flower clusters; J, scarlet sage (*Salvia splendens*), a popular ornamental mint with racemose inflorescence. (Drawings by Edna S. Fox.)

corolla, two or four stamens, and a deeply four-lobed ovary. The individual flowers are not conspicuous, but they are usually aggregated into dense inflorescences, which simulate racemes or spikes but in most cases are actually close axillary cymes. The flowers are irregular, complete, and hypogynous. The five sepals are united at their bases to form a calyx tube, and the free lobes are sometimes irregular. The upper lip of the sympetalous corolla is two-lobed, and the lower lip three-lobed. The five petals are coalesced below to form a well-developed corolla tube. The four stamens are attached to the corolla. The compound pistil is composed of two carpels, indicated by the two-lobed style. The superior ovary, however, is four-lobed at the summit, each lobe separating from the others at maturity and ripening into a one-seeded achene, or nutlet.

A rather high ranking for this family is indicated by the coalescence of sepals into a calyx tube, of petals into a corolla tube, and of the two carpels into a compound pistil, by the irregular corolla, the reduction of the number of carpels and stamens, and the attachment of the stamens to the corolla tube. The hypogynous nature of the flower is a primitive character.

Family Rosaceae (Rose Family). The family Rosaceae (Fig. 314), named for the genus *Rosa*, includes about 70 genera and 1,200 species of trees, shrubs, and herbs distributed over a wide geographical range. Species of the Rosaceae are found from the Arctic to the Antarctic Circles, and from sea level to high mountain peaks. They reach their greatest development in the temperate zones. Such herbaceous forms as cinquefoil, dewberry, and raspberry, and tree-like forms such as hawthorns, wild crab apple, June berry, and wild cherry are commonly found in meadows or forests. The family includes many ornamentals and fruit trees and is therefore of considerable economic importance. Among the ornamentals may be mentioned roses, spiraeas, flowering apples, almonds, and cherries. The pome fruits (apples, pears, and quinces), the common stone fruits (cherries, apricots, plums, and peaches), blackberries, strawberries, loganberries, raspberries, and dewberries are all members of the Rosaceae.

The members of this family exhibit considerable diversity in structure and form both of vegetative organs and of flowers. The leaves are spirally arranged on the stem, usually have stipules, and range from simple, as in some of the tree forms, to pinnately compound forms, as in the roses. A few genera have palmately compound leaves. The flowers are mostly regular and perfect, and in nearly all cases are complete. In one section of the family (cherry, plum, and peach group) the flowers are perigynous (Fig. 314, C). In strawberries, blackberries, raspberries, and a number of others, the floral tube is not so evident and the calyx lobes are correspondingly longer. In the pear, the apple, the quince, and the hawthorn (Fig. 314, A), the flowers are epigynous.

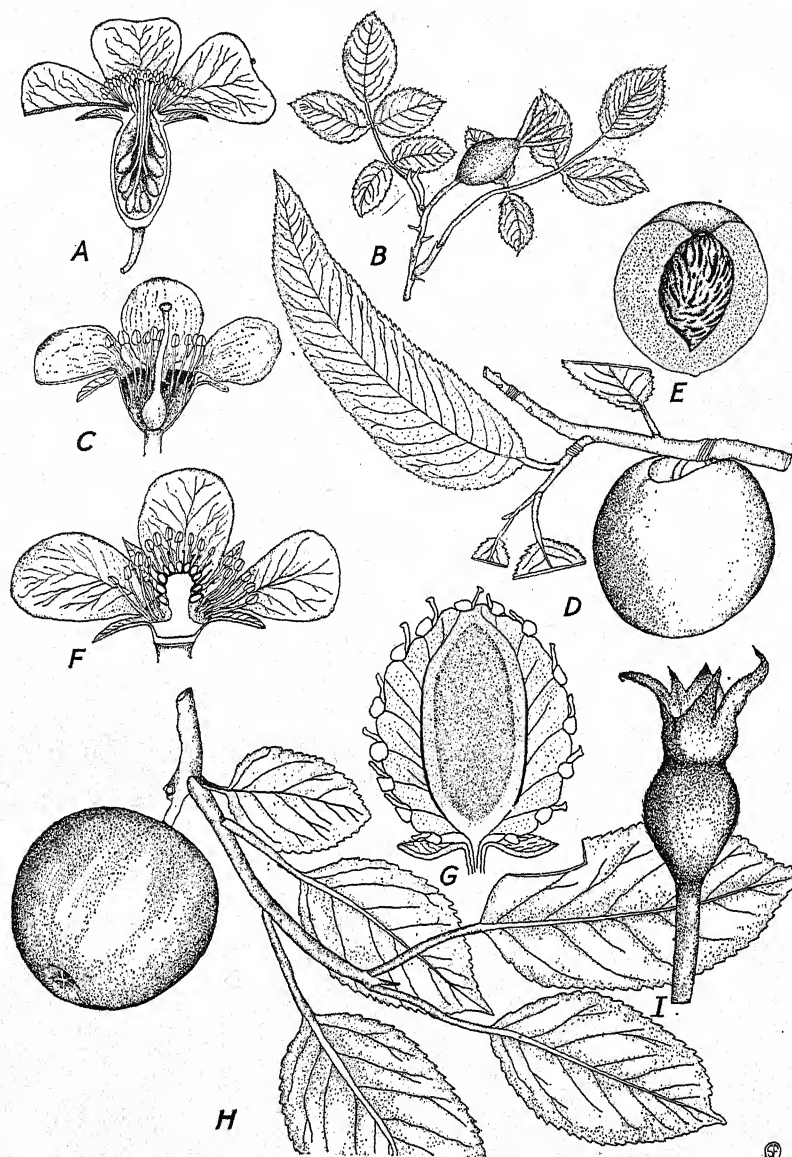


FIG. 314. The rose family (Rosaceae). A, flower of rose cut vertically, showing the numerous centrally placed pistils, the numerous stamens, and calyx and corolla; the flower is regular and epigynous; B, leaves and fruit of rose; the persistent appendages at the apex of the fruit are calyx segments; C, the perigynous flower of peach cut vertically; D, fruit and leaf characters of peach; E, peach fruit cut vertically, showing structure; F, vertical section of strawberry flower, showing the numerous simple separate pistils covering the surface of a conspicuous receptacle; G, fruit of strawberry cut vertically, showing the many fruitlets borne on the surface of a well-developed mass of receptacle tissue; H, fruit and leaves of apple; I, young apple fruit. (Drawings by Edna S. Foz.)

There are usually five sepals coalesced at the base and five petals that are always free from each other above and on the floral tube. Occasionally, as in cinquefoil, there are five smaller sepal-like outgrowths alternating with the larger calyx lobes and giving the appearance of 10 sepals. The stamens are several to many in number and are borne with the petals on the floral tube. The pistils vary in number from one to many. Cherries, plums, and peaches have but a single one-carpellate pistil, bearing usually a single ovule. Apples usually have a pistil composed of five carpels, the styles alone being free. In roses, blackberries, raspberries, and strawberries (Fig. 314, *F*), the pistils are numerous and distinct from each other.

There is great diversity among the members of this family as regards the type of fruit developed. In *Spiraea*, the fruit is a follicle with few to several seeds. In *Geum*, *Potentilla*, and related genera, each of the pistils, of which there may be one to several, ripens into an achene, as in many members of the Ranunculaceae. Strawberries, raspberries, and blackberries develop aggregate fruits. In the strawberry, the edible part of the fruit is the enlarged, fleshy receptacle (Fig. 314, *G*). The individual carpels in this case become achenes. In the blackberry and in the raspberry, the individual pistils ripen into drupelets. The rose fruit, or "hip" (Fig. 314, *A, B*), is an aggregation of achenes surrounded by the floral tube, which becomes fleshy. The fruit of the plum, the peach, and the cherry is a drupe; that of the pear, the apple, the quince, and the hawthorn is a pome.

The family is characterized by the relatively primitive feature of numerous and indefinite numbers of stamens and pistils that occur in many genera, by the more advanced condition of perigyny and epigyny, and by the diversity of its fruit types.

Family Leguminosae (Pea Family). The legume family (Fig. 315) is one of the largest families of seed plants. The name Leguminosae is derived from the type of fruit produced by members of the family, which is a legume. The family contains about 12,000 species in about 500 genera, widely distributed from the tropics to the arctic regions, being quite abundant in temperate zones and especially numerous in the tropics. Few families of dicotyledons are of greater economic importance. Some of the members of this family have been cultivated by man since remote antiquity. Prominent among the food plants in this family are peas, beans, lentils, and peanuts. The clovers, vetches, and alfalfa rank with our most important forage crops. Wistaria, lupine, mimosa, lotus, sweet peas, the Judas tree, and many others are important as ornamentals. The black locust and a few other species are used as timber. In addition, many of its species are used by bees in making honey. The plants of this family



FIG. 315. The legume family (Leguminosae). A-D, the redbud or Judas tree. A, flower cluster, appearing before the leaves expand; B, the slightly irregular flower with 10 stamens and a single pistil; C, leaf and fruit; D, fruit opened to show seeds; E-G, black locust; E, leaf and a single pistil; F, flower cluster; G, flower cut vertically; note the single pistil, half of the stamen sheath, and the single free stamen; H, *Aragallus Lambertii*, one of the "loco weeds" of the western ranges; I, a small alpine clover (*Trifolium Parryi*); J, single flower of *T. Parryi*. (Drawings by Edna S. Fox.)

also add to the nitrogenous content of the soil through the bacteria which commonly live in their roots. The family also includes many drug plants such as licorice and senna. Few of them are troublesome weeds, although the "loco" weeds of the Western ranges are poisonous to livestock.

The members of the Leguminosae may be herbs, shrubs, or trees. The leaves are usually spirally arranged, have stipules, and are nearly always compound, some palmately compound, as are the clovers, and others pinnately compound, as are beans and peas. The flowers are, in general conspicuous and have a fairly uniform structure (Fig. 315, *F*). They are usually hypogynous or sometimes perigynous, irregular, perfect, and complete. The arrangement of the floral organs is always cyclic. The calyx consists of five or four sepals that are more or less united. The corolla has five petals and in most species is irregular, as in the sweet pea. The Kentucky coffee tree and the honey locust have regular flowers, and in the Judas tree the flowers are only slightly irregular. In those species with strongly irregular flowers, the large upper petal is called the standard, the two lateral petals are the wings, and the two lower petals are united along one edge to form the keel. The stamens are usually 10 in number, 9 of which, in most cases, are laterally united to form a thin sheath around the pistil, while the tenth is free (Fig. 315, *G*). The most characteristic feature of the family is the pistil, formed of a single carpel with a superior ovary which on ripening becomes a pod, which is usually a legume. It commonly opens into two valves and exposes the few to many seeds (Fig. 315, *D*). Occasionally the pod is segmented into transverse, one-seeded sections or joints, sometimes covered with hooks or spines. This type of fruit is called a loment. In the peanut, the pod does not split open at maturity. Other minor variations occur.

The advanced features of the family are indicated by the reduced and usually constant numbers of the floral organs, by the beginning of coalescence of the petals, and by the bilateral symmetry of the flowers. The rather general hypogyny of the group, however, is a more primitive feature.

Family Umbelliferae (Carrot Family). The scientific name of the family (Fig. 316) is derived from the fact that the characteristic type of inflorescence is the umbel; the common name comes from the common name of an important species of the family, the carrot. The Umbelliferae include about 270 genera and 2,700 species, inhabiting for the most part the temperate climates of the Northern Hemisphere. Common in waste places are the wild parsnip, aniseroor, water hemlock, poison hemlock, cow parsnip, angelica, and wild carrot (Queen Anne's lace). The roots of the water hemlock (*Cicuta maculata*) contain an alkaloid known as cicutin, which is poisonous to livestock. Poison hemlock (*Conium maculatum*) is said to be the plant from which the extract which caused the death of



FIG. 316. The carrot family (Umbelliferae). A-D, water hemlock (*Cicuta maculata*); A, leaf and flowers; B, a single flower, showing inferior ovary, five stamens, and two styles; C, flower with corolla removed; D, cross section of the two lightly attached carpels, showing the single ovule in each carpel; oil ducts are indicated in the ovary walls; E-G, sweet cicely (*Osmorhiza longistylis*); E, leaf and fruits; F, a single fruit consisting of two loosely united ovarian segments; G, cross section of the fruit, shaded portion representing the seed in each ovarian segment; H-J, pennywort (*Hydrocotyle umbellata*); H, entire plant; I, a single flower; J, a single fruit. (Drawings by Edna S. Fox.)

Socrates was obtained. Poisonous alkaloids and medicinal drugs are obtained from a number of species. Members of the family which furnish food for man are the garden carrot, a derivative of the wild carrot, and celery. Parsley, caraway, anise, and dill furnish aromatic oils valuable as flavorings.

The members of this family are, for the most part, herbaceous though rarely somewhat woody, and include annuals, biennials, and perennials. Carrots, parsnips, and other biennials develop fleshy taproots the first year and flowers and fruits the second. The pinnately compound, spirally arranged leaves usually lacking stipules, but with large sheathing leaf bases, and the hollow, conspicuously jointed stems are outstanding vegetative characters of the family.

The flowers, characteristically borne in either simple or compound umbels, are small and usually yellow or white. They are regular, perfect, complete, and epigynous in nearly all cases. The calyx is visible only as five minute teeth at the apex of the ovary. The five separate petals and the five stamens, over which the petals are commonly curved inward, are inserted at the top of the ovary. The pistil is bicarpellate. The fruit is characteristic of the family and is called a schizocarp (Fig. 316, *D*). It consists of two one-seeded mericarps which separate at maturity, each one remaining suspended for a while by a slender stalk. The outer walls of these seed-like fruits are usually marked with prominent longitudinal ridges, between which are located tubes containing aromatic oils. Frequently hooked prickles or hairs are present. In shape, they vary from nearly spherical fruits to the more common elongate and often flattened type.

Family Compositae (Sunflower Family). The Compositae (Figs. 317 to 320) represent one of the highest levels of development found in the plant kingdom. The family received its name from the composite nature of its inflorescence, which is usually a head consisting of many closely compacted individual flowers, the whole structure being commonly mistaken for the flower. It is one of the largest families of seed plants, consisting of at least 850 genera and more than 15,000 species and has practically a world-wide distribution. The large production of seed and the efficient devices for dispersing the seeds in the group have contributed toward making many of its species the most troublesome of weeds. Common among these are the ragweeds, burdock, cocklebur, fleabane, Spanish needles, *Galinsoga*, yarrow, dogfennel, all the true thistles, chicory, wild lettuce, dandelion, hawkweeds, daisies, asters, and goldenrods. A few species like white snakeroot and cocklebur are poisonous to livestock. In addition, the pollen of many of them, notably the ragweeds and the goldenrods, has long been known to cause hay fever. On the other hand,

few families of dicotyledons are better known as ornamentals. Asters, chrysanthemums, zinnias, coneflowers, sunflowers, dahlias, cornflowers, and marigolds are among the oldest and best known of garden flowers. Lettuce and the artichoke are probably the best known food plants in the group.

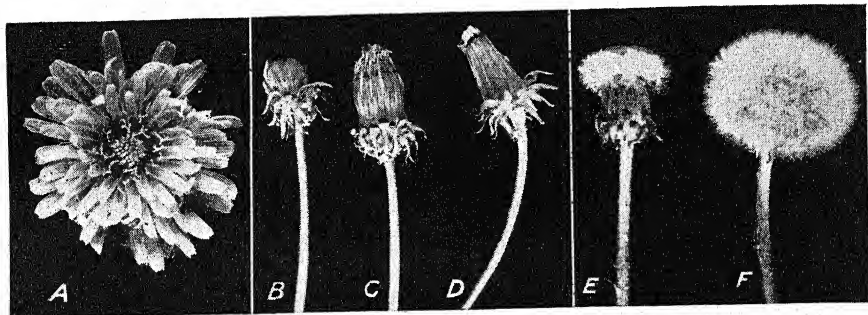


FIG. 317. The dandelion. A, the open inflorescence (head); B-D, the head enclosed by the involucre bracts representing successive closed periods of the head during the maturation of the flowers and fruits; E, head beginning to open as the fruits are maturing; F, fruits ready for dissemination.

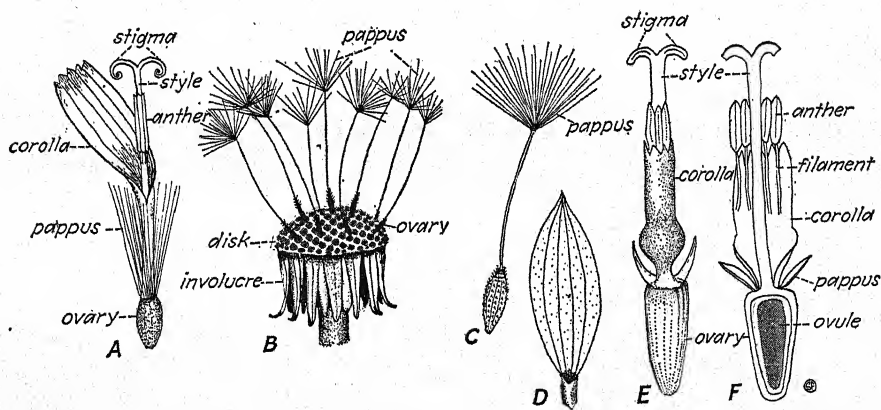


FIG. 318. Flower structure in Compositae. A-C, details of dandelion flower and fruit; A, single flower of dandelion removed from head; B, head of dandelion after most of the fruits are disseminated; C, single fruit of dandelion; D-F, details of flower of sunflower; D, a sterile marginal ray flower, consisting of only corolla; E, a disk flower; F, a disk flower with corolla split vertically to show stamen attachment, and the ovary cut vertically to show the single ovule. (Drawings by Edna S. Fox.)

Most of the members of this family are herbaceous plants. Some are annuals, some biennials, and others herbaceous perennials. The sagebrushes of the Western dry-land areas are often shrubby in growth, and a few species are tree-like. The leaves may be opposite, spiral, or whorled, simple or compound. The flowers are fairly uniform in spiral structure, and

in all cases the inflorescence is a head. The structure of the dandelion head may be taken as fairly representative of the structure of the inflorescence characteristic of the whole family.

The dandelion head is composed of a large number of separate and distinct flowers (Fig. 317, *A*). It is borne on a long, hollow, leafless stalk or scape, and is subtended by two series of green, lanceolate or linear bracts, known as the involucre, which is often erroneously thought to be a calyx when the whole head is mistaken for a flower (Fig. 317, *B-E*). A vertical section through the center of the head reveals the small, individual yellow flowers attached to the upper flattened portion of the scape. Each of these flowers is perfect and complete (Fig. 318, *A*). The ovary is distinctly inferior. A circle of minute white hairs at the apex of the ovary, known as the pappus, is believed to represent the calyx lobes, the basal part of the calyx forming the outer part of the floral tube, which is adnate to the ovary wall. Surmounting the ovary is the yellow corolla which, for a short distance upward, is in the form of a tube but emerges into a strap-shaped, yellow, lateral blade which is five-toothed at the apex. These five parts are the coalesced petals. Composite flowers of this type are said to be ligulate, *i.e.*, tongue-shaped, and the corolla is obviously irregular. Coming up through the tube-like lower portion of the corolla is the style. At its apex it is forked into two minute recurved stigmas. Somewhat below these stigmas and closely sheathing the style are the five very small anthers cohering laterally. Their filaments can be discerned extending downward into the corolla tube to which they are attached. The dandelion flower is therefore epigynous; the calyx is represented by the pappus, and the corolla is irregular, consisting of united petals; five stamens are present, attached within the corolla tube, closely sheathing the style, their anthers coalesced; the pistil is bicarpellate as indicated by the two stigmas, but only a single ovule is present.

After all the flowers of the head have opened, the bracts of the involucre turn slowly upward and inward, compressing the head into a conical shape (Fig. 317, *C, D*). In this condition, the head remains for several days until the fruits are mature. As this is taking place, a very small beak, bearing the pappus at the apex of the ovary, begins to elongate and pushes the pappus upward until it occupies the apex of a long thread-like stalk connected in its turn to the apex of the ovary (Fig. 318, *B, C*). The fruits are now ready for dissemination, the involucre again recurves or is thrown back, and the white dandelion seed head is exposed (Fig. 317, *E, F*). Each fruit loosens from its point of attachment, and the white feathery pappus is caught up by the wind and thus the fruit with its one enclosed seed is borne away.

In certain other members of the family, only the marginal flowers have

the strap-shaped corolla seen in the dandelion head (Fig. 319, *B*). Sunflowers and coneflowers illustrate this type of head. These marginal flowers may be entirely sterile (Fig. 318, *D*), or they may be only pistillate. The inner flowers in such cases are much smaller than the marginal ones

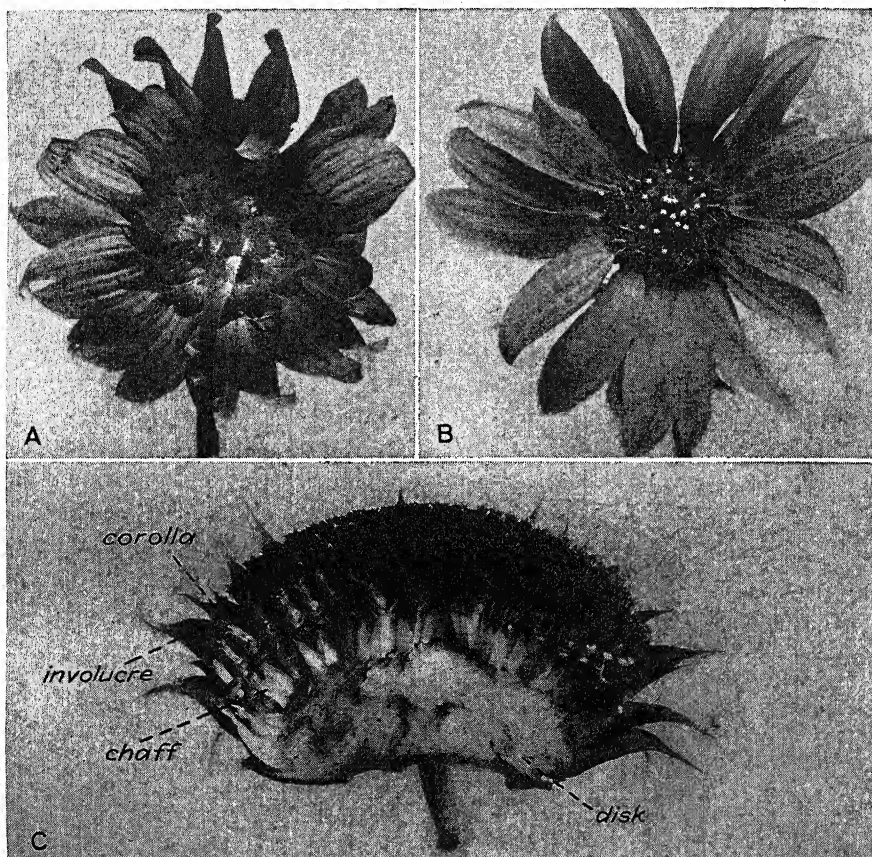


FIG. 319. The sunflower head. *A*, view of underside of head, showing the series of involucre bracts and the petals of the marginal ray flowers; *B*, view of head from above; the marginal flowers are ray flowers and are sterile; the center is composed of numerous regular disk flowers with protruding stigmas; *C*, sunflower head after ray flowers have withered, the head being broken open here and some of the many disk flowers removed to show the disk, the chaff, and the individual flowers. Stigmas and styles have withered.

and in them the corolla is regular and five-toothed (Fig. 318, *E*, *F*). Flowers of this type are known as disk flowers, and the marginal ones are known as ray flowers. Otherwise, the structure of the individual flowers of sunflower shows little variation from that of dandelion. The

calyx is represented by two scales at the top of the ovary (Fig. 318, *E*, *F*). An additional series of scales, known as the chaff, is present subtending the individual flowers on the much enlarged disk (Fig. 319, *C*).

The features of the Compositae which give this family its high rank are (1) the grouping of the flowers into compact heads, (2) epigyny, (3) the coalescence of the petals to form a corolla tube, (4) the irregular corolla of the ligulate flowers, (5) the coherence of the anthers, forming a sheath around the style, and (6) the reduction in number of carpels to two with only a single ovule developing.

The "Amentiferae." Family Salicaceae (Willow Family). The families of dicotyledons thus far described are thought to represent a progressive evolution along several lines beginning with the Ranunculaceae. The

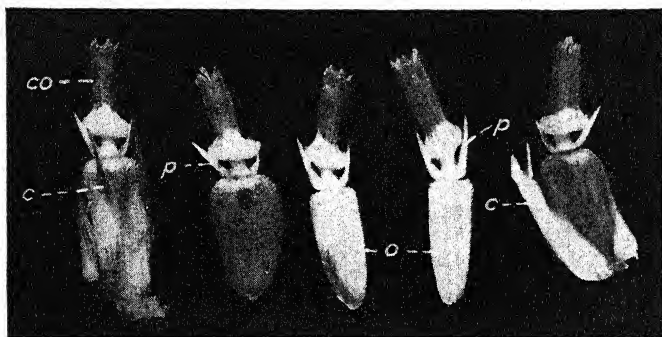


FIG. 320. A series of flowers from the sunflower head after anthers, stigmas, and styles have withered; *c*, chaff; *co*, corolla; *o*, ovary; *p*, pappus.

so-called Amentiferae or ament bearers (Figs. 321, 322), on the other hand, once regarded as the most ancient of the dicotyledons, are now usually considered to be simplified or reduced forms, possibly developed from an ancestral type having more floral parts. In general, the floral structures are simpler than those of the Ranunculaceae. The group is not a natural one and consists of a number of families, the most prominent of which are the beech family (Fagaceae), which includes beeches, oaks, and chestnuts; the birch family (Betulaceae), including alders, birches, and hazelnuts; the walnut family (Juglandaceae), comprising the walnuts and hickories; and the willow family (Salicaceae), which includes the willows, poplars, and aspens. All of them are trees or shrubs. The willow family is selected as a representative of this group of plants. It is probably to be regarded as the final step in the reduction thought to be displayed by the whole group.

The family Salicaceae includes but two genera and about 200 species. The two genera are the willow genus (*Salix*) and the poplar or aspen genus

(*Populus*). They are confined almost exclusively to the temperate and colder regions. Economically, they are not of first importance, although they are used to some extent as ornamentals, as windbreaks, and as pulpwood for papermaking. Some species of willow are cultivated for basket-making. The bark and leaves of other species furnish the glucoside salicin. Poplars will often grow in sections of the country where it is difficult to induce other trees to grow.

While many of the species of this family grow to be tall trees, most of the willows are of small stature. The leaves are spirally arranged, simple, and provided with stipules that are usually deciduous. The flowers, in common with other members of the so-called Amentiferae, are borne in catkins

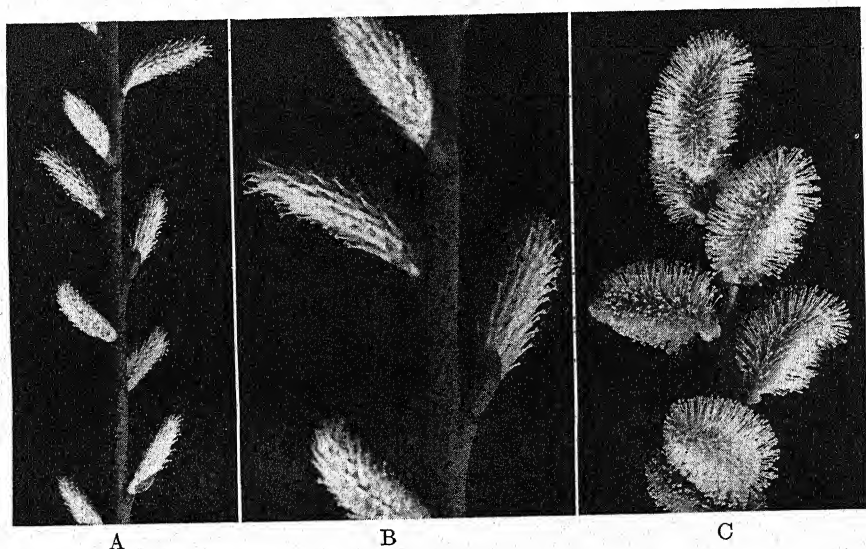


FIG. 321. Catkins of willow. A, pistillate catkins; B, same, enlarged; C, staminate catkins.

(aments) (Fig. 321), those of the willows being often erect, and those of the poplars and aspens drooping. The flowers are entirely imperfect, and the catkins are of two kinds, one with only staminate flowers and the other with only pistillate flowers. Furthermore, the two kinds of catkins are borne on different plants, *i.e.*, the species are dioecious. Each staminate flower of the willow is borne in the axil of a scale-like bract. No perianth is present, the flower consisting of but two (sometimes three or more) stamens (Fig. 322, A). The pistillate flower is also without a perianth and consists of a single bicarpellate pistil borne in the axil of a scale-like bract, with the apex of the style divided into two to four stigmas (Fig. 322, B). These flowers, as well as those of all other Amentiferae, are

almost entirely wind-pollinated. Since the individual flower of the willow consists of only a few stamens or a single pistil, it is obvious that, if reduction in floral structure has occurred, it has been carried almost to the lowest possible extreme in this family. In the aspens, however, there is

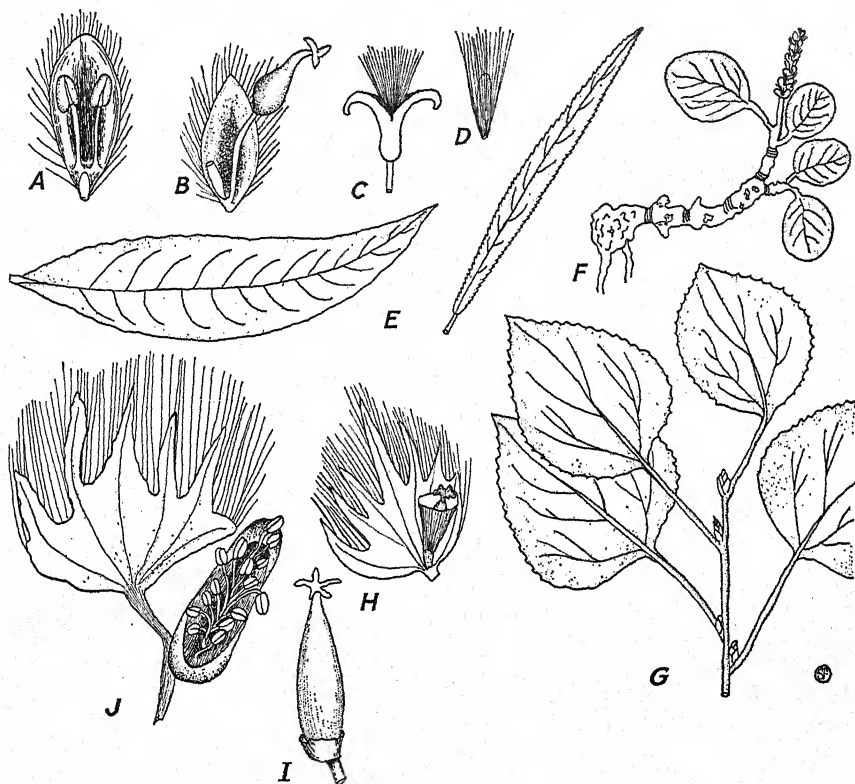


FIG. 322. The willow and aspen family (Salicaceae). A-F, willow; A, single staminate flower, consisting of two stamens and a minute nectar gland in the axil of a hairy bract; B, single pistillate flower, consisting of a single stalked pistil and a minute nectar gland in the axil of a hairy bract; C, mature fruit of willow splitting into valves; D, seed; E, variations in willow leaves; F, a small alpine willow from alpine regions of Rocky Mountains; G-J, aspen; G, twig and leaves of trembling aspen; H, single pistillate flower with rudimentary vase-like perianth and a single pistil in the axil of a hairy bract; I, single mature pistil; J, single staminate flower with numerous stamens in a boat-like perianth, in the axil of a hairy bract. (Drawings by Edna S. Fox.)

a rudimentary cup-like perianth present, and the number of stamens per flower is considerably larger (Fig. 322, H-J). The fruit is a small capsule dehiscent into two to four valves (Fig. 322, C). The numerous seeds (Fig. 322, D) are small and are enveloped by many fine hairs by which they are readily carried by the wind.

FAMILIES OF MONOCOTYLEDONS

Family Liliaceae (Lily Family). The family Liliaceae (Fig. 323) includes some of the best known members of the monocotyledons. The group is a large one, embracing nearly 200 genera and 2,500 species of wide distribution, but reaching its best development in the warmer regions of the temperate zones. Ornamental plants belonging to this family are common, particularly as spring flowers. These include hyacinths, tulips, lilies, lily of the valley, star of Bethlehem, day lily, dogtooth violets, Spanish bayonet, Solomon's seal, and trilliums. The death camas (*Zygadenus venenosus*) (Fig. 323, *N*) is the cause of serious sheep poisoning on Western ranges. Other species are known to have poisonous or medicinal properties. Asparagus and onions are well known as food plants.

Nearly all members of the family are herbaceous, but some are shrubs and a few are trees. Many of them are perennials, and, of these, numerous species produce bulbs or corms by which they are propagated. The leaves, as in all monocotyledonous plants, are typically parallel-veined. Exceptions are found in the trilliums and the cat briers. The flowers are perfect, regular, and hypogynous. The calyx and the corolla, each consisting of three separate parts, usually resemble each other. Six stamens surround the compound pistil made up of three carpels. The fruit is commonly a capsule or a berry.

The reduced and constant number of floral organs in the Liliaceae indicates a higher development than is shown by the Ranunculaceae. The similarity of calyx and corolla, both being petaloid, is also thought to be an advanced feature.

Family Orchidaceae (Orchid Family). With at least 500 genera and 15,000 species, the orchid family (Figs. 324, 325) probably ranks with the composite family in number of species; yet the plants are seldom abundant in any locality. Although numerous forms occur in temperate regions, the family reaches its greatest development in the tropical rain forests where the plants are commonly epiphytic, often growing on tree trunks or branches. Large numbers of aerial roots are produced by such forms, some of which serve as organs of attachment and others as organs for the absorption of moisture from the humid atmosphere. Absorption is facilitated by the presence of several external layers of dead cells with a high water-absorbing capacity, these layers constituting the **velamen**. A few species of the temperate regions lack chlorophyll and hence must live either as saprophytes or parasites. Orchids are the best known and of the greatest economic importance because of the rare beauty and striking form of the flower (Fig. 324). Even the less spectacular species native to the cooler temperate regions, such as the moccasin flower and the showy orchid, are sought after and in many localities have been exterminated.



FIG. 323. The lily family (Liliaceae). A-C, the wild yellow lily (*Lilium canadense*). A, upper and median portion of stem, and a single terminal flower; B, maturing ovary; C, ovary cut crosswise to show the three locules; D-H, the small Solomon's seal (*Polygonatum biflorum*); D, upper part of plant with axillary flowers; E, a single flower; F, flower with perianth split vertically; G, mature fruit; H, cross section of ovary; I, false Solomon's seal (*Smilacina racemosa*), upper part of plant with racemose panicle; J-M, false lily of the valley (*Maianthemum canadense*); J, entire plant with racemose inflorescence; K, a single flower; L, fruits; M, cross section of a single fruit; N-O, the death camas (*Zygadenus venenosus*); N, entire plant in flower; O, a single flower; P, the painted trillium; Q, *Lloydia serotina*, a common liliaceous plant of arctic and alpine regions. (Drawings by Edna S. Fox.)

Orchid flowers occur either solitary or in spikes or racemes. They are highly irregular, complete, and epigynous (Fig. 325, *B, C*). The perianth, composed of three sepals and three petals alternately arranged, is usually entirely petaloid. The lower petal, known as the lip, or labellum, is en-



FIG. 324. A *Cattleya* orchid, the most popular of the greenhouse orchids. Note aerial roots hanging over side of basket and showy, irregular flower. (Drawing by Elsie M. McDougle.)

tirely unlike the other two in form, size, and color. It is more or less sac-like and forms the "moccasin" or "slipper" of the moccasin flower or lady's-slipper. In some species, it is the most conspicuous and largest part of the corolla. The filaments of the three stamens are usually fused with the pistil to form the column, at the apex of which one or two anthers occur. In *Cypripedium*, the third stamen is developed into a petaloid

structure that covers the column. The compound pistil consists of three carpels. The ovary is inferior. The fruit is a capsule containing myriads of extremely minute seeds.

Few families show a greater reduction in number of parts or a greater fusion of parts than is exhibited by the orchids. They are among the highest developed monocotyledons as regards floral structure; yet, the separate petals and the many seeds in the fruit are relatively primitive features.

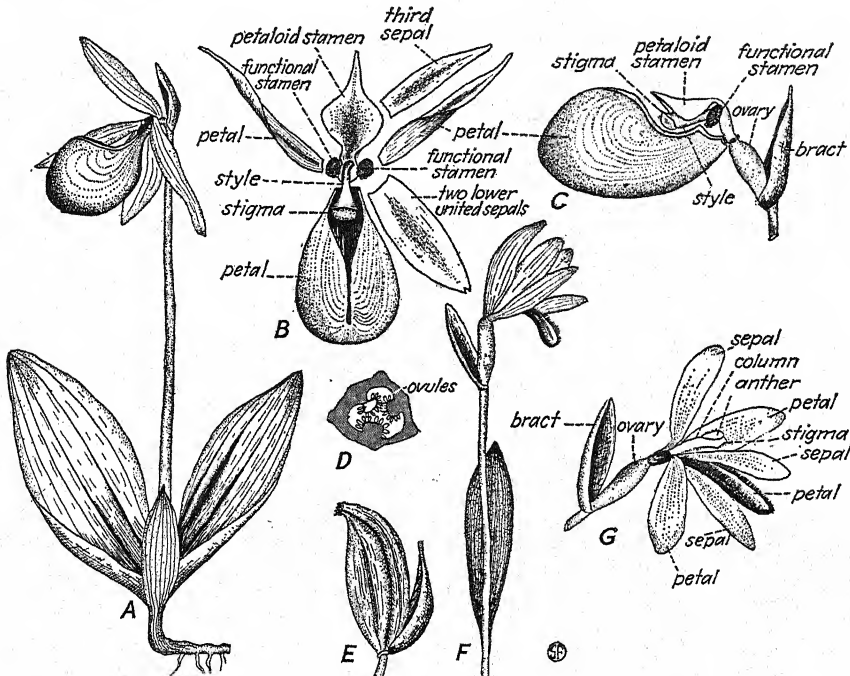


FIG. 325. The orchid family (Orchidaceae). A-E, moccasin flower (*Cypripedium acaule*); A, entire plant, in flower; B, C, flower dissected to show parts, B, in front view, and, C, in side view with sepals and two petals removed; D, cross section of ovary; E, mature fruit; F-G, rose pogonia (*Pogonia ophioglossoides*); F, upper part of plant with terminal flower; G, the flower. (Drawings by Edna S. Fox.)

Family Gramineae (Grass Family). The grasses (Figs. 326, 327) are probably the most widely distributed and the most numerous, from the standpoint of individuals, of all seed plants. About 400 genera and 4,500 species are known, ranging from the equator to the frigid zones. Some of the members of this family were probably the first plants cultivated by man. No other family is of greater economic importance. To the Gramineae belong all the cereals, including corn, wheat, oats, barley, rice, and rye, many of the most important forage crops, such as timothy,

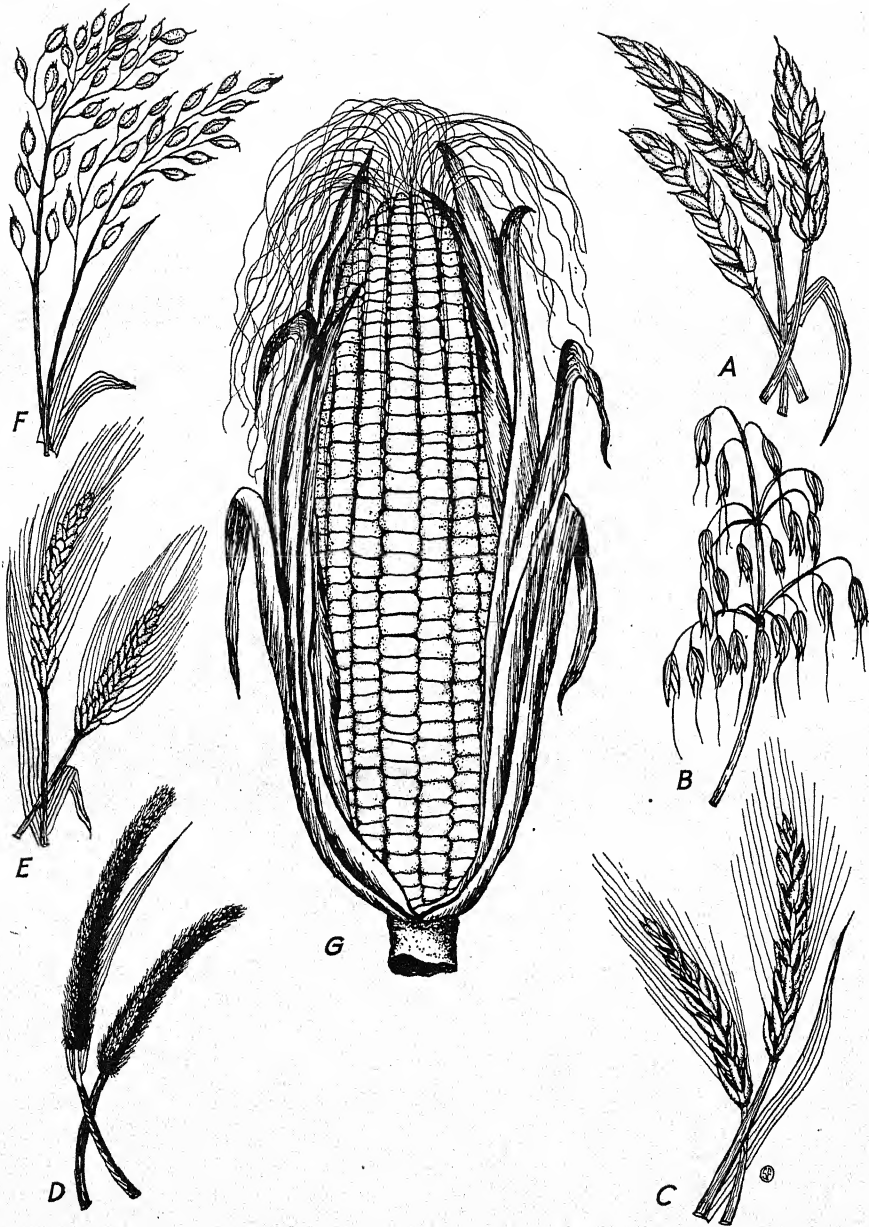


FIG. 326. Inflorescences of seven of the most important members of the grass family. *A*, wheat; *B*, oats; *C*, rye; *D*, timothy; *E*, barley; *F*, rice; *G*, corn. (Drawings by Edna S. Fox.)

Kentucky bluegrass, Sudan grass, millet, and sorghums, as well as the numerous lawn grasses, and sugar cane. Many forms become noxious weeds and are extremely difficult to eradicate. Johnson grass, old witch grass, foxtail grass, sandbur, quack grass, and wild barley belong to this category.

While an occasional tree-like species, notably the bamboo, is found in the tropics, grasses are usually herbaceous and often perennial. The stems are cylindric, hollow, and conspicuously jointed. Corn and sugar cane, however, have solid stems. The long ribbon-like leaves, with parallel venation, are spirally arranged on the stem, their bases modified into sheaths which surround the stem and usually extend from the nodes at which they are attached to the next node above.

The inflorescence is a spike, a raceme, or a panicle (Fig. 326). To the main axis of the inflorescence, termed the **rachis**, or to its branches, are attached the spikelets of flowers (Fig. 327). The axis of the spikelet is termed the **rachilla**. Each spikelet bears a succession of chaff-like bracts, sometimes known as **glumes**. The two lowermost glumes, and sometimes the uppermost one, are empty. Each of the others bears a single flower in its axil and is called a flowering glume, or **lemma**. There may be one or many flowering glumes in each spikelet. The flowering glumes often bear awns or are bearded on the external surface, as in rye, barley, and bearded wheats. On the axis of the flower itself, and just above the attachment of the flowering glume, is borne another bract known as the **palea** or **palea**.

The perianth consists of two or three minute, scale-like structures called **lodicules** at the base of the ovary. There are usually three (but sometimes one, two, or six) stamens and (if the species is one with perfect flowers) a single compound pistil consisting of three carpels, only one of which functions. There are only two (rarely three) feathery stigmas and two short styles. The ovary contains a single locule and bears a single ovule. At maturity, the seed coat is fused to the pericarp, forming the typical fruit of the grasses, which is a grain, or caryopsis.

The grasses are among the most difficult of all seed plants to identify, chiefly because of the small size and great reduction in the floral organs, and because the sterile and fertile glumes add confusion. As in the willow family, the flower is thought to be reduced until it consists essentially of only stamens and a pistil or, in the case of imperfect flowers, of only stamens or only a pistil. The grasses are thought to represent the apex of a reduced evolutionary line of monocotyledons.

Family Typhaceae (Cattail Family). The cattail family (Figs. 328, 329) is one of the smallest of the angiosperms, containing but a single genus, *Typha*, and about 10 species, only three of which are found in the

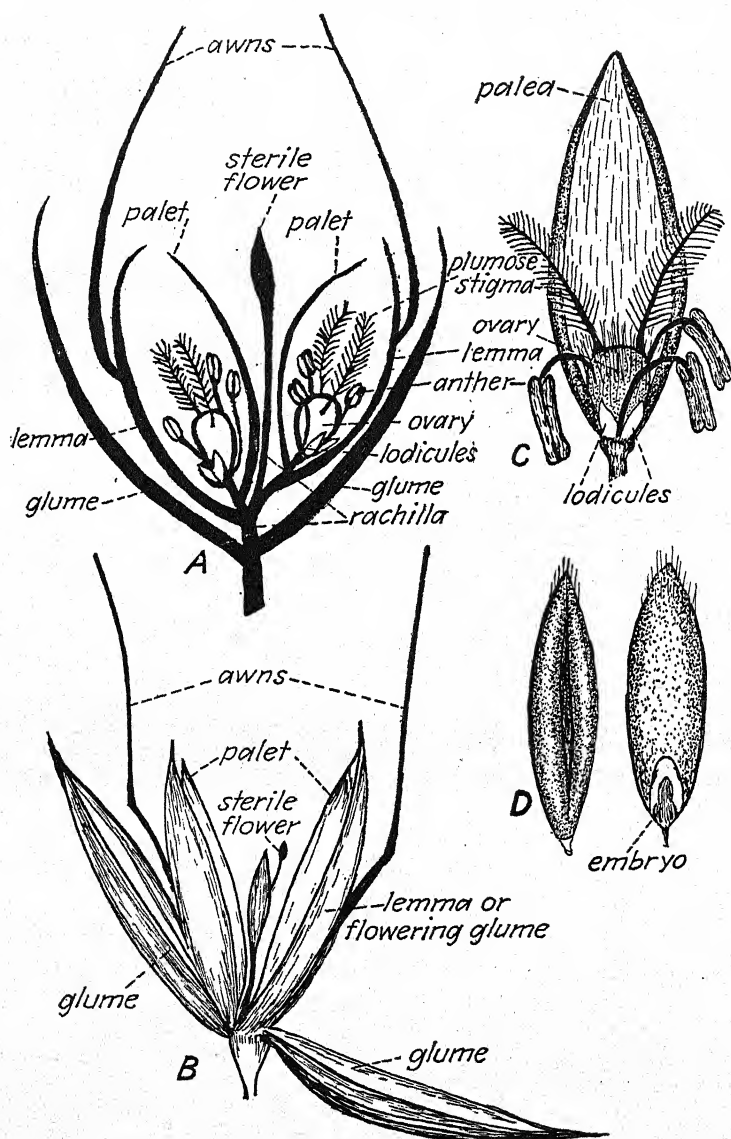


FIG. 327. The grass family (Gramineae). Oats (*Avena sativa*). A, diagrammatic representation of a spikelet of oats with two fertile flowers and one sterile flower; B, enlargement of a single spikelet; C, enlargement of a single flower with palea behind; D, oat grain or caryopsis after removal of lemma and palea, the one to right showing the embryo side. For the entire inflorescence of oats, see Fig. 326, B.

United States. They are plants of wet or marshy situations, always growing in colonies. They are herbaceous perennials with underground stems, or rhizomes. The leaves are long, narrow, and parallel-veined as in most monocotyledonous plants. Their bases form conspicuous overlapping sheaths.

The plants are monoecious, bearing their flowers in a very dense spike with the evanescent staminate flowers above and the persistent pistillate flowers below (Fig. 328). The spike is borne at the apex of the aerial

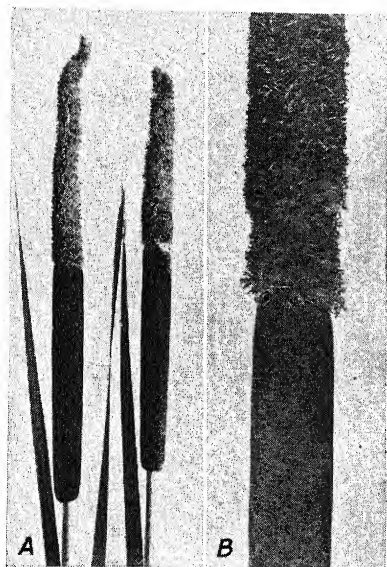


FIG. 328.

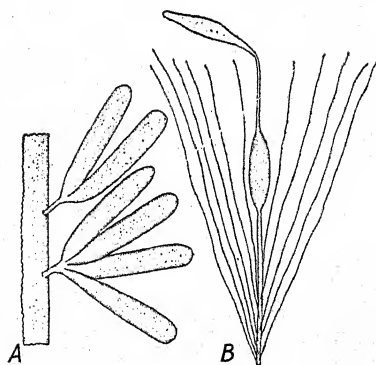


FIG. 329.

FIG. 328. The cattail family (Typhaceae). The common cattail (*Typha latifolia*). A, two flowering stalks, the staminate flowers on the upper part of each; B, portion of an inflorescence more magnified.

FIG. 329. The flowers of cattail. A, two staminate flowers, one of two stamens and one of four; B, a single pistillate flower, the stalked ovary surrounded by bristly hairs.

stem and overtops the leaves. Each staminate flower consists of from two to seven stamens united at the base to a common, short filament (Fig. 329, A) and usually accompanied by numerous bristly hairs. Similarly, each pistillate flower (Fig. 329, B) consists of but a single, simple pistil on a short stalk with a cluster of bristly hairs at its base. These hairs are considered to be a perianth. There is a long, slender style (sometimes two) terminated by a somewhat flattened stigma. Pollination is effected entirely by wind. The simple pistil contains a single ovule. The pistillate flowers are densely crowded on the spike and are mingled with numerous sterile flowers. Soon after flowering, the staminate

flowers wither and fall off, leaving the naked axis on which they were borne projecting above the pistillate portion of the spike. The latter gradually assumes a dark-brown color and a velvety appearance as the fruits slowly ripen. The bristly hairs of the pistillate flowers persist in the fruit and aid in its dissemination.

The cattail family, like the Amentiferae and the grasses, is thought to have developed by a process of reduction, resulting in the simplified flowers just described.

CHAPTER 20

HEREDITY

Historical Introduction. The modern study of heredity begins with the publication in 1866 of a paper by Gregor Mendel, an Austrian monk. In this paper the author reported the results of some very important experiments in heredity. Somehow, the full significance of these experiments was not comprehended by scientists until some years later (about 1900) when they were rediscovered and confirmed independently by DeVries, Correns, and Tschermak, European biologists; it was Bateson, a British zoologist, who through his publications was largely instrumental in bringing Mendel's conclusions to the general attention of biologists. In his investigation of the inheritance of the somatic characters of the common garden pea, Mendel established certain definite principles which have since been shown to be applicable to a great diversity of organisms, both plant and animal, including man. In fact, since 1900, the results of investigations of inheritance in a large number of plants and animals have so uniformly supported the fundamental principles of heredity which Mendel established that they have come to be regarded as some of the great generalizations of biological science.

The Facts of Heredity. In his study Mendel selected plants showing contrasting characters, such as tall pea plants and dwarf pea plants, plants bearing red flowers and plants bearing white flowers, and plants producing smooth seed as contrasted to plants producing wrinkled seed. His method of experimentation was to mate plants which differed in one pair only of these contrasting characters, *e.g.*, tall plants mated with dwarf plants. Later in his experiments he mated plants which differed in regard to two or more pairs of contrasting characters, *e.g.*, tall plants bearing smooth seed mated with dwarf plants bearing wrinkled seed.¹

¹ Artificial mating in plants is accomplished by removing the stamens from the flower of the plant to be used as the female parent. The stamens are removed before the anthers have opened to shed the pollen. This operation, called emasculation or castration, prevents "selfing," or the pollination of the flower by its own pollen. The emasculated flower is covered by a paper bag to prevent its natural pollination. Several days later pollen from the anthers of the plant to be used as a male parent is placed on the stigma of the emasculated flower. Viable seed produced by this method will produce hybrid plants. This method is also known as hybridization or more colloquially as making a "cross."

The offspring resulting from the matings, or "crosses" as they are often called, are referred to as the **F₁ generation**, or first filial generation of hybrids. In such hybrids, it was found that often only one of the contrasting characters appeared in the F₁ hybrid. That is, in a cross between tall pea plants and dwarf pea plants all the F₁ hybrids were tall plants (Fig. 330). Mendel called the parental trait which thus appeared in the F₁ generation the **dominant** trait or character. The parental trait which did not appear in the F₁ hybrids he called the **recessive** trait. Tallness is therefore dominant over dwarfness in peas.

When the seeds produced by tall dominant F₁ hybrids were planted, the second filial generation or the **F₂ generation** of hybrids was obtained. A very interesting result was observed by Mendel in the F₂ generation of hybrids. He discovered that both of the original parental traits were to be found in the plants of the F₂ generation. There were some tall pea plants and some dwarf pea plants in the F₂ generation. The tall plants were apparently exactly like the original tall plants of the parental strain and the tall plants of the F₁ hybrid generation. The dwarf pea plants were apparently exactly like the original dwarf plants of the parental strain. These tall and dwarf plants were, however, not equally numerous. In every F₂ generation studied, there were about three times as many dominant tall plants as there were recessive dwarfs. Mendel found F₂ totals of 787 tall and 277 dwarf plants, *i.e.*, 2.84 tall to 1 dwarf or approximately a 3:1 ratio from all crosses.

Mendel studied the third filial generation of hybrids grown from seeds produced on the F₂ hybrid plants. Seeds from the dwarf F₂ pea plants produced all dwarf plants; *i.e.*, they were pure for the recessive dwarf trait. One-third of the tall F₂ pea plants (or one-fourth of the total F₂ population) bore seed which produced tall F₃ plants; *i.e.*, they were pure for the dominant tall trait. Two-thirds of the tall F₂ pea plants (or one-half of the total F₂ population) showed by this breeding test that they were not pure for either the tall or the dwarf trait. The seeds from this group of plants produced tall plants and dwarf plants in the ratio of three tall plants to one dwarf plant. This behavior indicated that they were actually like the original F₁ hybrids as regards their breeding qualities, for the original F₁ hybrid produced a 3:1 ratio as regards tallness and dwarfness.

The Physical Basis of Heredity. Mendel believed that there must be some material substance in the germ plasma or gametes, which was related in some way to the development of each somatic trait he studied. Mendel's reputation as one of the great biologists of modern times rests upon the fact that he formulated a theory of the behavior of the hereditary factors. This theory is in accord not only with observed phenomena of breeding but with the facts which have recently been learned about the behavior of the chromosomes in the reproductive cells.

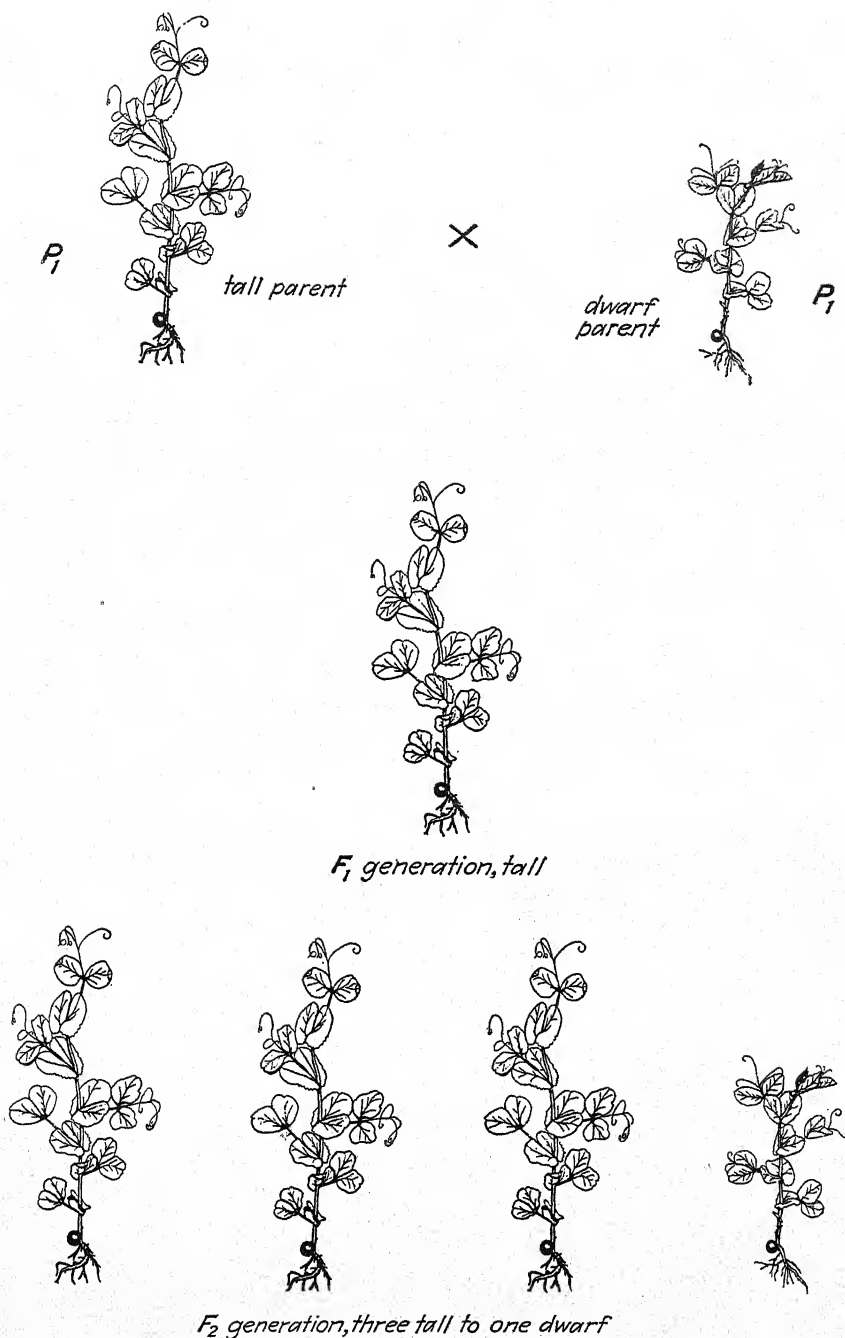


FIG. 330. Inheritance in tall and dwarf peas; above, the tall and dwarf parents (P_1); center, the tall first-generation (F_1) hybrid; below, the two classes of the second generation (F_2), consisting of three tall plants and one dwarf plant.

The presentation in 1900 of Mendel's original work stimulated a great revival of interest in the study of heredity and led directly to the establishment of the experimental method in this field.

The scientific study of the problems of heredity by experimental methods, which have been in vogue since that time, combined with a careful study of the behavior of the cells of the germinal tracts of plants and animals at the time of reproduction, has made possible the expansion of Mendel's original theory into one of the most important generalizations of biological science.

The most important feature of this generalization is the conception that the factors determining hereditary characters are associated with the chromosomes of every cell in the body (pages 19 to 24). Since these hereditary factors are inseparably associated with the chromosomes, they move with them through all the cell divisions of the maturation processes which lead in plants to spore production (and in animals to the production of gametes). The union of the gametes at fertilization brings the chromosomes from each parent, with their associated hereditary factors, into the fertilized egg (zygote) which is to develop into a new individual of a new generation. In this way the hereditary factors pass from generation to generation. The behavior of the chromosomes during meiosis and fertilization, especially, forms the **physical basis** of the behavior of the factors which determine or influence the development of hereditary characters (Fig. 331). This conception of the relations of hereditary factors to the chromosome is known as the chromosome theory of heredity and is now widely considered as offering the most plausible explanation of the observed facts of heredity.

In this theory, the hereditary unit, or material substance most closely related to the development of a trait, is assumed to be located in the chromosomes. This material is called a **determiner**, a hereditary **factor**, or a **gene**. Genes are thought to occur in pairs. A recent term **allele**, pronounced *al-leel*, emphasizes the paired relationship of the genes. Each gene is the allele of the other, and the two genes constitute a pair of alleles, or allelic genes. Since the genes are located in the chromosomes, their passage from one generation to another is dependent upon the passage of the chromosomes by the gametes from one generation to the following.

In other portions of this text, it has been emphasized that meiosis is responsible for the reduction of the number of chromosomes characteristic of the diploid, or $2N$, condition to that characteristic of the haploid, or $1N$ (pages 517 to 520). Meiosis is important not only in making possible a change in the chromosome number from $2N$ to $1N$. Certain chromosome relationships are emphasized to present other aspects of the significance of meiosis, especially those important in heredity.

At the time of reproduction (pages 616 to 630) in most organisms, both plant and animal, each gamete, as the result of meiosis, has the reduced or haploid ($1N$) number of chromosomes (Fig. 331). This collection of chromosomes may be designated as a "set" of chromosomes. There is a set of chromosomes in the egg and a set of a corresponding number in the sperm. Since these have been derived from the two parents, they may be designated, respectively, the female set of chromosomes and the male set of chromosomes. When fertilization or the union of the sperm with the egg occurs, the resulting zygote has therefore received two sets of chromosomes, one a male set and the other a female set. These sets normally contain the same number of chromosomes, *i.e.*, the haploid number characteristic of the species, and the zygote resulting from the fertilization has the number characteristic of the diploid ($2N$) condition for that species.

In each cell of the pea plant there are 14 chromosomes. This number is the $2N$ or diploid number. When the maturation processes occur in the microsporocytes, or microspore mother cells, in the anthers and in the megasporocytes, or megaspore mother cells, in the ovules of a pea plant, meiotic divisions occur which reduce the number of chromosomes from the diploid number of 14 to the haploid number of 7. It will be recalled from the fundamental biological principles learned in the study of the seed plants that, following the maturation divisions in the anthers, microspores are formed from the microsporocytes, or microspore mother cells (pages 616 to 619). Each microspore in the pea plant will have the haploid number of 7. The microspores develop pollen tubes, each containing two sperms, or male gametes, with the haploid number (7) of chromosomes. Likewise, in the ovule the megasporocyte, or megaspore mother cell, with the diploid number of 14 chromosomes, as a result of the maturation processes, forms four megaspores each with the haploid number (7) of chromosomes. A megaspore in each ovule develops a female gametophyte, all cells of which contain the haploid number of chromosomes. One cell of this female gametophyte is the egg, or female gamete, which also has 7 chromosomes.

When the gametes of the tall pea plant are formed, they have 7 chromosomes, one of which bears a gene conditioning tallness. Likewise, when the gametes of the dwarf pea plant are formed, they have 7 chromosomes, one of which bears a gene for dwarfness. When the cross is made between the tall pea plant and the dwarf pea plant, the gametes of the tall plant fuse with the gametes of the dwarf plant. This process is termed fertilization and the cell resulting from the fusion is known as the zygote. In peas, several zygotes may be formed as a result of each cross, as indicated by the several peas in a pod (Fig. 332). Each zygote develops into an

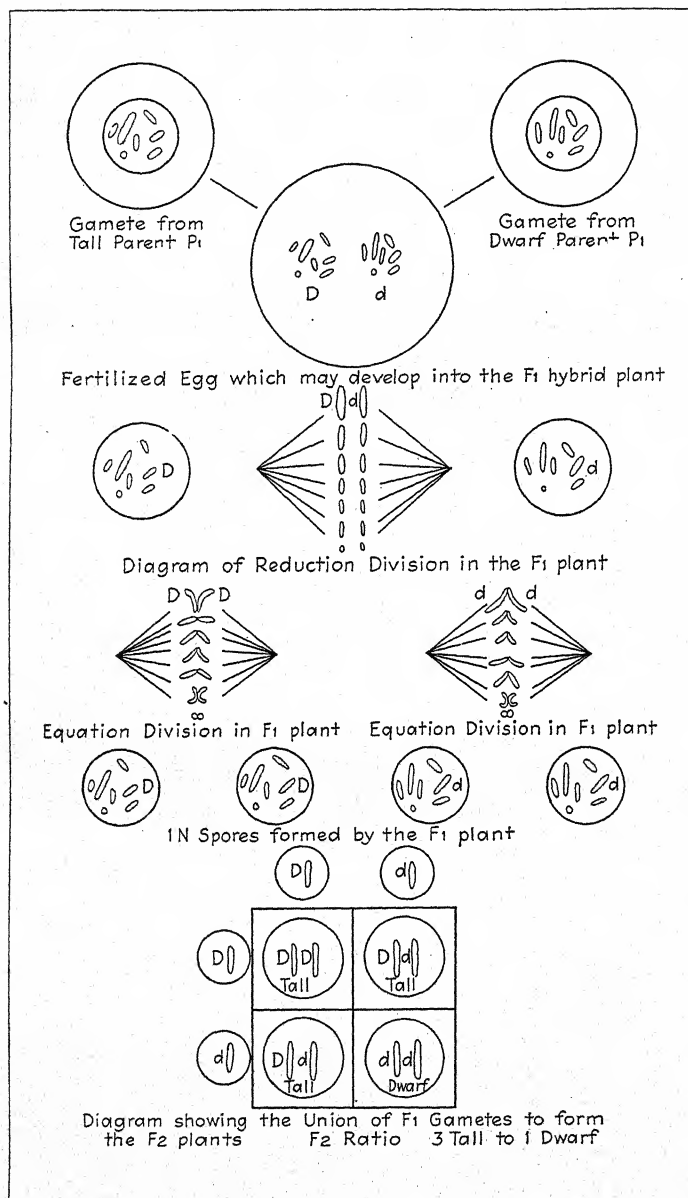


FIG. 331. Diagrammatic representation of the relation of genes to chromosomes and their behavior in inheritance; *above*, gametes of parents P₁, uniting to form the fertilized egg which will develop the first hybrid generation F₁; *center*, the two maturation divisions; during this process the homologous chromosomes are separated and the genes *D* and *d* are also separated (segregation); these processes finally result in the production of spores (which eventually will form the gametes) from the F₁ hybrid; *below*, the recombination of genes as a result of self-fertilization in the F₁ hybrid; the checkerboard shows the four classes of F₂ progeny; *D*, the gene conditioning tall; *d*, the gene conditioning dwarf.

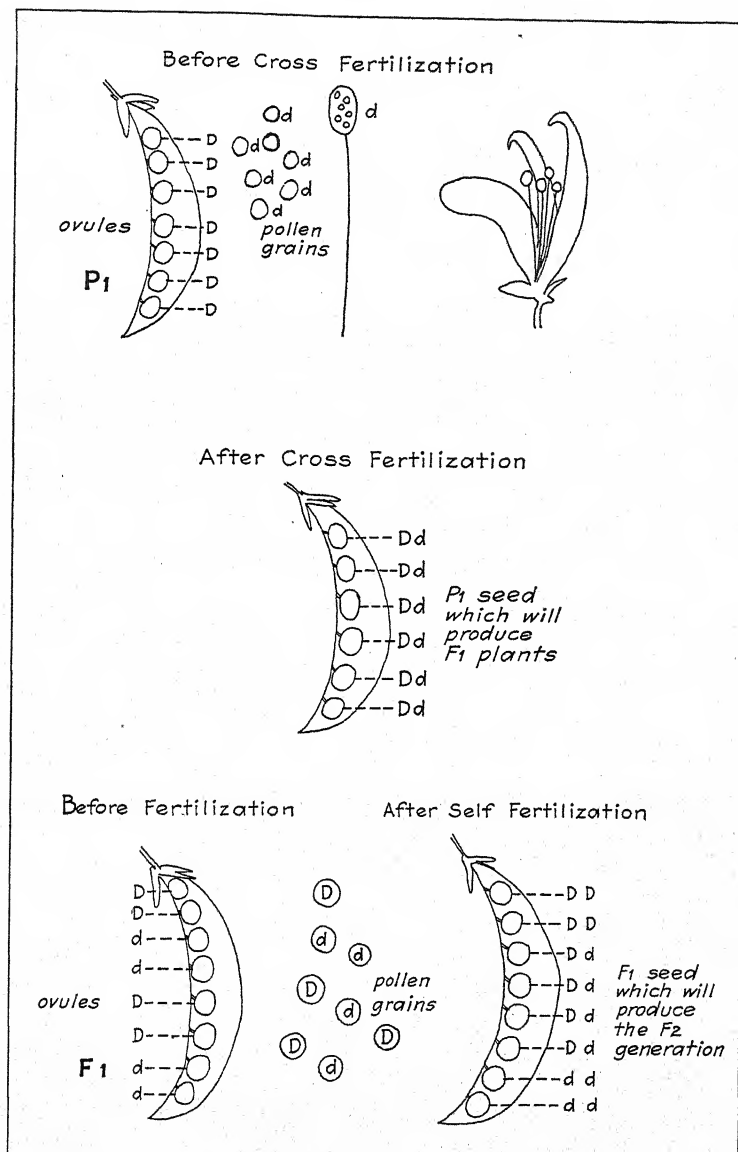


FIG. 332. Diagrammatic representation of the production of the F_1 and F_2 generations in peas; *above*, the flower, stamen, pollen grains, and ovary with ovules of the parent pea plants before fertilization; D , tall, d , dwarf; *center*, the pea pod on the female parent after fertilization. Each ovule contains an embryo with both genes D and d . These embryos will grow into tall F_1 hybrid plants. *Below left*, ovules in pod of pea of F_1 plant. As a result of the segregation of genes during the maturation processes, each ovule contains the gene D or d , never both of them. Likewise, pollen grains contain either D or d . *Below right*, the ovules in the pea pod of F_1 plant. As the result of recombination, seeds contain the genes DD , Dd , or dd . The embryos in the seeds (ovules) will produce the F_2 generation of three tall peas to one dwarf pea.

embryo, the embryo into a seedling, the seedling into an adult plant which, upon reaching maturity, produces flowers, pollen, ovules, and gametes. Each gamete bears a set of 7 chromosomes, the egg a set of 7, and the sperm a set of 7. Not only are these chromosomal sets alike in number but each chromosome of each set has a mate in the set from the gamete of opposite sex (Fig. 331). That is, each chromosome of the set of 7 in the egg has a corresponding mate in the set of 7 in the sperm. These pairs of chromosomes are called **homologous chromosomes** or **synaptic mates**. The two members of a pair of homologous chromosomes are generally alike in shape, size, general characteristics, and, what is more important genetically, they carry allelic genes determining or **conditioning** the same character or contrasting characters. In the pea plant, there is, therefore, a pair of chromosomes (synaptic mates) which carry genes having to do with the height of the plant—tallness or dwarfness. For example, in the pea the pair of homologous chromosomes each may carry the gene determining tallness or both may carry the gene determining dwarfness or one member of the pair may carry the gene for tallness and the other the gene for dwarfness.

When hybridization is desired between two strains or varieties of animals or plants, it is accomplished by mating representative individuals of these two strains. These individuals then become the parents (P_1) of the desired hybrid (F_1). The gametes of the parent individuals carry genes, or factors in certain of the chromosomes, which are responsible for the hybrid condition of the offspring. For example, in the crossing of tall pea plants with dwarf pea plants, a factor for dwarfness, represented by d , is carried in one of the chromosomes in the pollen grains from the dwarf plant. As the pollen tube and finally the gametes (sperms) are formed, this factor d passes along with the chromosome. Likewise, in the ovules, the megaspores contain a chromosome bearing the factor for tallness D . As one of the megaspores finally develops into the embryo sac containing an egg, or female gamete, this factor passes along with the chromosome to the gamete (pages 618 to 623). The chromosomes which carry these two factors D and d are two members of a pair of homologous chromosomes. The union of the male set of 7 chromosomes with the female set of 7 provides the nucleus of the zygote with 14 chromosomes. The gene for tallness D and the gene for dwarfness d are, therefore, both present in the nucleus of the zygote. This zygote by growth and cell division develops into an embryo within the seed. When the seed is planted, the embryo develops first into a seedling and finally into an adult **hybrid** pea plant. It has been found that these plants which are the result of hybridizing two parents differing in height are all tall, resembling in this respect the tall parent entirely. It is said that the gene for tallness D is

dominant over the gene for dwarfness d , which therefore is recessive. Both genes, D , the one for tallness, and, d , the one for dwarfness, are present in every cell of the whole F_1 hybrid plant. The gene for dwarfness, however, does not manifest itself in any way during the life of the F_1 hybrid.

Upon attaining maturity, the tall F_1 hybrid pea plant undergoes the maturation processes which include meiosis leading to the production of microspores and megaspores (Fig. 331). During this process the number of chromosomes is reduced from the diploid number 14 to the haploid number 7. Not only is the number of chromosomes reduced to the half number but in all normal meiotic divisions the two members of each of the seven pairs of homologous chromosomes, or synaptic mates, are separated from each other, passing to opposite poles of the division spindle and ultimately into different megaspores and microspores, from which they pass on into different gametes. Since the two genes D and d , for tallness and dwarfness, respectively, are carried in different members of a pair of homologous chromosomes, they too are carried apart at meiosis. This separation of the genes D and d , called the **segregation of allelic genes**, is the basis of **Mendel's first law of heredity**. This separation is of the utmost importance, for it ensures that these genes, derived from different parents and associated together in the F_1 hybrid, are finally completely separated and pass into different gametes. Although the genes D , conditioning tallness, and d , conditioning dwarfness, have been associated throughout the life of the F_1 hybrid plant, they separate during meiosis. This separation is complete without any contamination of one gene by the other. After such association, the gene D is still just as pure for tallness as it was earlier when it was in the pure tall parent. Likewise, the gene d , conditioning dwarfness, is pure and uncontaminated by gene D .

The pea plant is what has been termed a **self-pollinated** plant; *i.e.*, the pollen from the anthers of a flower falls naturally on the stigma of the same flower. Following this, by the development of the pollen tube and the production of the gametes, **self-fertilization** occurs. In the F_1 hybrid pea plant, therefore, self-fertilization may normally be expected. There are two kinds of eggs produced, *viz.*, those bearing the gene for tallness D and those bearing the gene for dwarfness d . Likewise, there are two kinds of sperms formed, those with the gene for tallness D and those with the gene for dwarfness d . At the time of fertilization, these two kinds of male and two kinds of female gametes unite by chance. In this way one-half of the eggs carrying the D gene may by chance be fertilized by sperms bearing a d gene. Likewise, the eggs carrying the d gene may by chance be fertilized by sperms one-half of which bear the D gene and one-half the d gene. The resulting zygotes may, therefore, have the following **recombination** of the D and d genes: DD , Dd , dD , and dd . These zygotes

develop into embryos, seedlings, and ultimately adult plants and compose the second generation of hybrids, the F_2 . Since the gene for tallness D is fully dominant over the gene for dwarfness d , all plants receiving either two genes for tallness DD or one gene for tallness and one gene for dwarfness Dd will be tall. Those plants receiving two genes for dwarfness will be dwarf because there are no dominant genes present to overcome the dwarfing effects of the recessive genes. There are in the F_2 generation two classes of plants, *viz.*, tall plants resembling the original tall parent P_1 and dwarf plants resembling the original dwarf parent P_1 . These two classes of plants, not, however, numerically equal, occur in the ratio of three tall plants to one dwarf plant—3 tall:1 dwarf.

Monohybrid Ratios in Other Characters. Pea plants bearing round seeds in contrast with wrinkled ones have distinct hereditary units, or genes, that determine the dominant round trait. These genes may be designated RR , where R indicates the round trait. The allelic genes determining the contrasting recessive trait, wrinkled, may be indicated as rr . The seeds of peas differ in color as well as shape. There are dominant yellow-colored seeds and recessive green seeds. The allelic genes determining these contrasting traits are $Y-y$, where Y determines yellow and y the green color. The traits, round vs. wrinkled shapes and yellow vs. green colors, are characteristics of the embryos in the seeds. An embryo is really the young plant of the next generation.

Following hybridization of two pea plants, one bearing dominant round seeds, RR , and the other recessive wrinkled seeds, rr , the P_1 female plant produces pods containing all round seeds with heterozygous F_1 embryos, Rr . Self-fertilization of F_1 plants grown from these seeds produces pods with both round and wrinkled seeds, frequently with both types in one pod. The embryos in these seeds are RR , Rr , and rr in the ratio of 1:2:1; compare lower part of Fig. 332. Because of full dominance of R over r there will be three round seeds, 1 RR and 2 Rr , to one wrinkled rr . Furthermore, because the characteristics are traits of the embryo, hybridization involving dominant yellow, YY , and recessive green, yy , in peas yields three yellow to one green seed in the pods produced by selfed F_1 Yy plants.

Dihybrid Ratios. Combinations of two or more independently hereditary traits may occur in one organism, as, for example, tallness or dwarfness of plant with shape and color of seeds. Tall pea plants may bear either round or wrinkled seeds, which may be either yellow or green. Likewise, the seeds produced by dwarf pea plants may be round yellow, round green, wrinkled yellow, or wrinkled green, depending on the hereditary factors or genes.

Mendel, interested in learning whether two pairs of contrasting traits were independently inherited, crossed a pea plant bearing dominant round yellow seeds, *RRYY*, with one producing recessive wrinkled green seeds, *rryy*. Following this hybridization, seeds produced by the female plant all showed the dominant round yellow characteristics. The embryos within these seeds were heterozygous, *RrYy* for both pairs of genes, and were therefore **dihybrids**.

When these seeds were planted, their F_1 embryos developed into adult F_1 plants that eventually produced seeds. The seeds borne by the F_1 plants contained F_2 embryos and represented the F_2 generation with various recombinations of shapes and colors of seeds. Mendel found that the F_1 plants "yielded seeds of four sorts, which frequently presented themselves in one pod." In a total of 556 seeds, there were 315 round yellow, 101 wrinkled yellow, 108 round green and 32 wrinkled green seeds. This represents an approximate ratio of 9:3:3:1.

In seeking an explanation of the 9:3:3:1 F_2 ratio of traits found when parents that differ in two pairs of characteristics are crossed, it is essential to consider the relationship of the genes to the chromosomes. The relationship of genes to chromosomes is such that the gene *R* is located on a certain chromosome and the gene *r* is located on the other member of this pair of synaptic mates, or homologous chromosomes. Likewise, *Y* and *y* are located on the two members of another distinctly different pair of synaptic mates. During meiosis, the two members of a pair of synaptic mates separate each from the other. That is, the chromosome bearing the gene *R* separates from the chromosome bearing the gene *r*. At the same time, separation of the synaptic mates is occurring in all six pairs of the remaining chromosomes including the pair bearing the genes *Y* and *y*. The chromosome bearing the gene *Y* is separated from the chromosome bearing the gene *y*. This chromosome behavior results in the simultaneous segregation of the two pairs of genes *R-r* and *Y-y*. Since there is no relationship between the two pairs of synaptic mates, or pairs of homologous chromosomes, concerned, the accompanying segregation is called the **independent segregation** of two pairs (or more) of genes.

To gain the proper conception of the independent assortment of genes, it is essential to develop a mental picture of the actual chromosome behavior. In the nuclei of the several microsporocytes and megasporocytes, in the seven pairs of homologous chromosomes (in the pea plant), each chromosome is separated from its synaptic mate. This separation is simultaneous; all the chromosomes are separated at the same time during meiosis. One member of each pair of synaptic mates goes to each of the two poles of the division spindle. Since there is no relationship or attraction between these

chromosomes, the separation of each of the several pairs of synaptic mates is absolutely independent of all the others. Therefore, the segregation of the genes is also independent. This independent separation of synaptic mates leads to the **chance or free assortment** of the genes into the resulting

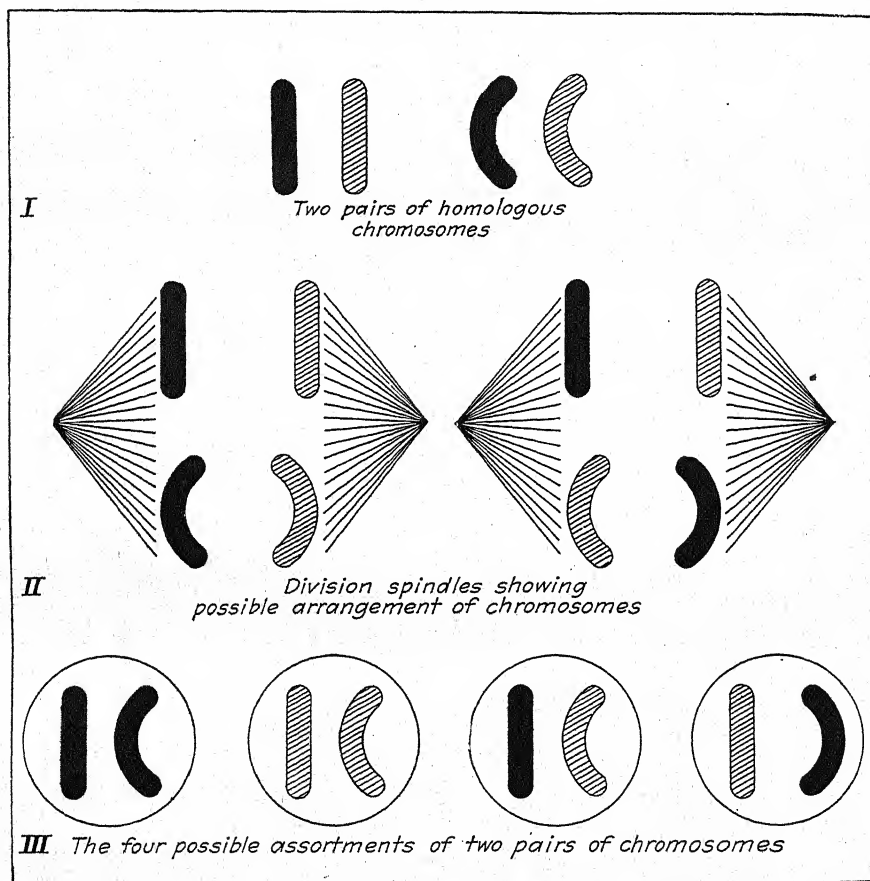


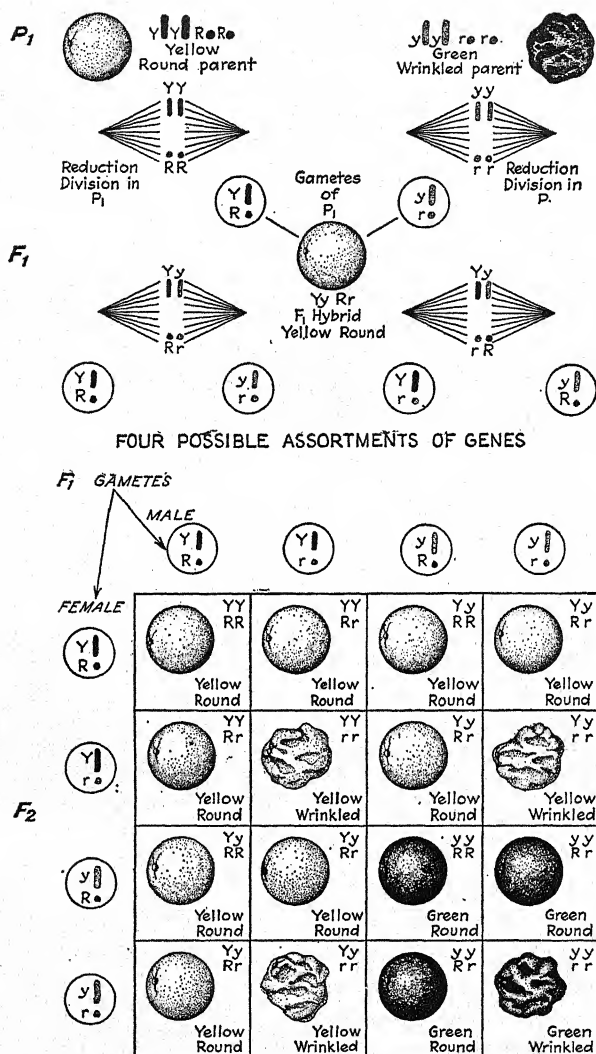
FIG. 333. Diagrammatic representation of the behavior of chromosomes during meiosis. The independent separation of the members of two pairs of homologous chromosomes constitutes the physical basis of Mendel's law of the independent segregation and assortment of genes. I, the chromosomes in the nuclei of any organism; II, the possibilities of chromosome arrangements on the division spindles during the maturation (meiotic) divisions; III, the possible assortments of chromosomes resulting from the divisions at II.

pollen grains and embryo sacs and finally, of course, into the gametes produced by the F_1 hybrid plant. Chance or free assortment is actually accomplished in the following manner (Fig. 333). The chromosome bearing the *R* gene and the chromosome bearing *Y* may go to the same pole of

the division spindle during the first meiotic division, leaving in this case their respective synaptic mates bearing r and y to go to the opposite pole. This behavior means therefore that ultimately R and Y will both be located in one gamete and that r and y will be located together in another gamete. There is, however, no relationship or attraction between these chromosomes. Accordingly, there is an equal chance that the chromosome bearing the gene R and the chromosome bearing the gene y may go to the same pole of the division spindle and the chromosome bearing the gene r and the chromosome bearing the gene Y will go to the opposite pole. This possibility of chance distribution of chromosomes to the poles of the division spindle results, therefore, in the chance or free assortment of the genes to the microspores and megaspores. Finally, gametes bearing the assortment of genes RY , Ry , rY , and ry are produced in equal numbers. The production of four kinds of gametes (as regards the genes they contain) is called the chance or free assortment of genes. The independent assortment of genes based upon the independent separation of two or more pairs of homologous chromosomes is Mendel's **second law of heredity**.

Reproduction in an F_1 plant, which is hybrid for two pairs such as round wrinkled seed and yellow-green seed described before, is accomplished when the female gametes, or eggs, which in equal numbers contain gene assortments of RY , Ry , rY , ry , are fertilized by sperms which in equal numbers contain the same gene assortments, *viz.*, RY , Ry , rY , ry (Fig. 334). There are equal chances for the union of any of the four kinds of sperms with any of the four kinds of eggs. The resulting recombinations of genes will produce an F_2 hybrid generation consisting of four classes of offspring, *viz.*, plants producing round yellow seed, round green seed, wrinkled yellow seed, and green wrinkled seed. While there are four classes of F_2 plants, the individual F_2 plants composing these classes are not equally numerous. There are nine RY (round yellow), three Ry (round green), three rY (wrinkled yellow), and one ry (wrinkled green). This F_2 ratio is due to the recombination of genes when the F_1 gametes unite at fertilization to produce the F_2 generation.

Incomplete Dominance of the Genes. Since Mendel's time, other investigators have found that genes do not always show **complete dominance** and **recessiveness** as exhibited in the case of tallness and dwarfness in peas. The genes determining or conditioning many characters are only **partly** or **incompletely dominant**. This is true in the cases of many bright-colored flowers such as red-flowered four-o'clocks. When plants such as the four-o'clock, bearing red-colored flowers, are crossed with plants bearing white flowers, the plants of the F_1 hybrid generation bear intermediate pink-colored flowers. In the F_2 generation, the ratio is 1:2:1, *i.e.*, one plant bearing red-colored flowers, two plants bearing pink



THE POSSIBLE RECOMBINATIONS OF GENES

FIG. 334. Diagrammatic representation of the simultaneous inheritance of two pairs of contrasting characters, yellow round peas and green wrinkled peas; *above*, the parents yellow round and green wrinkled, each with two pairs of homologous chromosomes with their allelomorphic genes, $Yy-Rr$; division spindles showing the separation of homologous chromosomes with their associated genes; *center*, the union of the parental gametes to form the F₁ hybrid producing the dominant yellow round pea; division spindles show the possibilities of chromosome arrangement on the spindles which will result in the independent assortment of genes in the four classes of spores finally produced; *lower*, the union of the four classes of male and female gametes as the result of self-fertilization; the checkerboard illustrates the 16 possible recombinations of genes in the F₂ generation; four classes of F₂ progeny are produced in the ratio of 9 yellow round, 3 yellow wrinkled, 3 green round, and 1 green wrinkled; there are 12 yellow to 4 green or 3:1 ratio and 12 round to 3 wrinkled or 3:1; each pair of contrasting characters behaves as a typical monohybrid.

flowers, and one plant bearing white flowers. The red- and white-flowered plants continue to breed true in succeeding generations, but the pink-flowered plants, being actually hybrids, in succeeding generations continue to segregate into the red-, pink-, and white-flowered plants in the ratio of 1:2:1.

These instances of **incomplete dominance**, now known to be very numerous, are due to the action of the genes. Neither the gene *w*, conditioning white-colored flowers, nor the gene *W*, conditioning red-colored flowers, is completely dominant or completely recessive when in hybrid combination as *Ww* in the F_1 generation. Both genes seem to react together, making a net or joint result of a condition of pink-colored flowers. Segregation of the genes during meiosis takes place as normally expected, *W* separating from *w*. Recombination at the time of fertilization results in the formation of one *WW* zygote which upon maturity produces red flowers, two *Ww* zygotes producing ultimately pink flowers, and one *ww* zygote producing white flowers.

Other Actions of Genes in the Development of Traits. Besides the allelic relationship of dominance and recessiveness, which may be either full or incomplete, genes may show other actions. Although generally recognized by its determination of some rather prominent trait, a single gene may influence the development of more than one character. As an example, certain genes may determine the development of color in the flower or in the seed and also influence the production of color in other parts of the plant, such as the stem or the leaves. In other cases, certain genes may determine the development of some visible characteristic like color or form and in addition interfere with some *vital function*. Genes that act in this way cause the death of the organisms that receive them. They are called **lethal genes**. Genes that act in this way usually yield a 2:1 F_2 ratio instead of the expected 3:1. This is because one of the organisms in each four dies as a result of the lethal action of the genes. It should be emphasized, however, that many genes which influence more than one trait are not lethal in their effects.

The Interaction of Genes in the Development of Characteristics. It is now recognized that many heritable traits are *dependent upon more than one gene*. Possibly every gene in the body exerts an influence in the development of every trait, with some one, two, or a few *major* genes having a predominant effect. Many cases are known in which a given characteristic is dependent upon two, three, or several distinct pairs of major genes. In these cases, the genes act to *complete*, *supplement*, or even *inhibit* the action of other major genes of the group. A group of genes acting together in this way is called a **gene complex**, and the **interaction** often results in the numerical modification of the expected mendelian ratios.

Some modifications of the ordinary F_2 dihybrid ratio of 9:3:3:1 are as follows:

9:7	13:3
9:3:4	12:3:1
9:6:1	15:1

Although the numerical relationships of visible traits are modified in the above ratios, *they constitute no exceptions to mendelian principles. Segregation, assortment, and recombination of genes occur regularly; the modifications of the ratio are the result of the action and interactions of the genes in the development of the visible characteristics.*

Linkage. During recent years, the investigation of the inheritance of the numerous characters of many different organisms, both plants

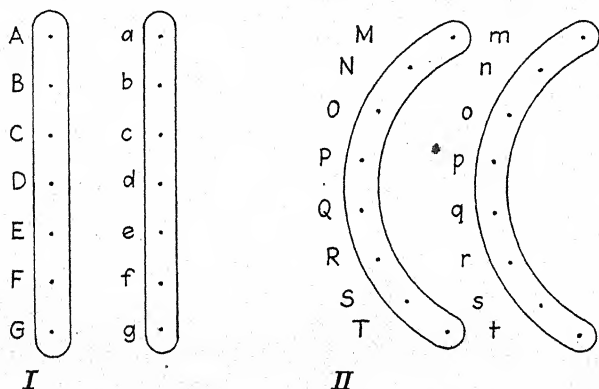


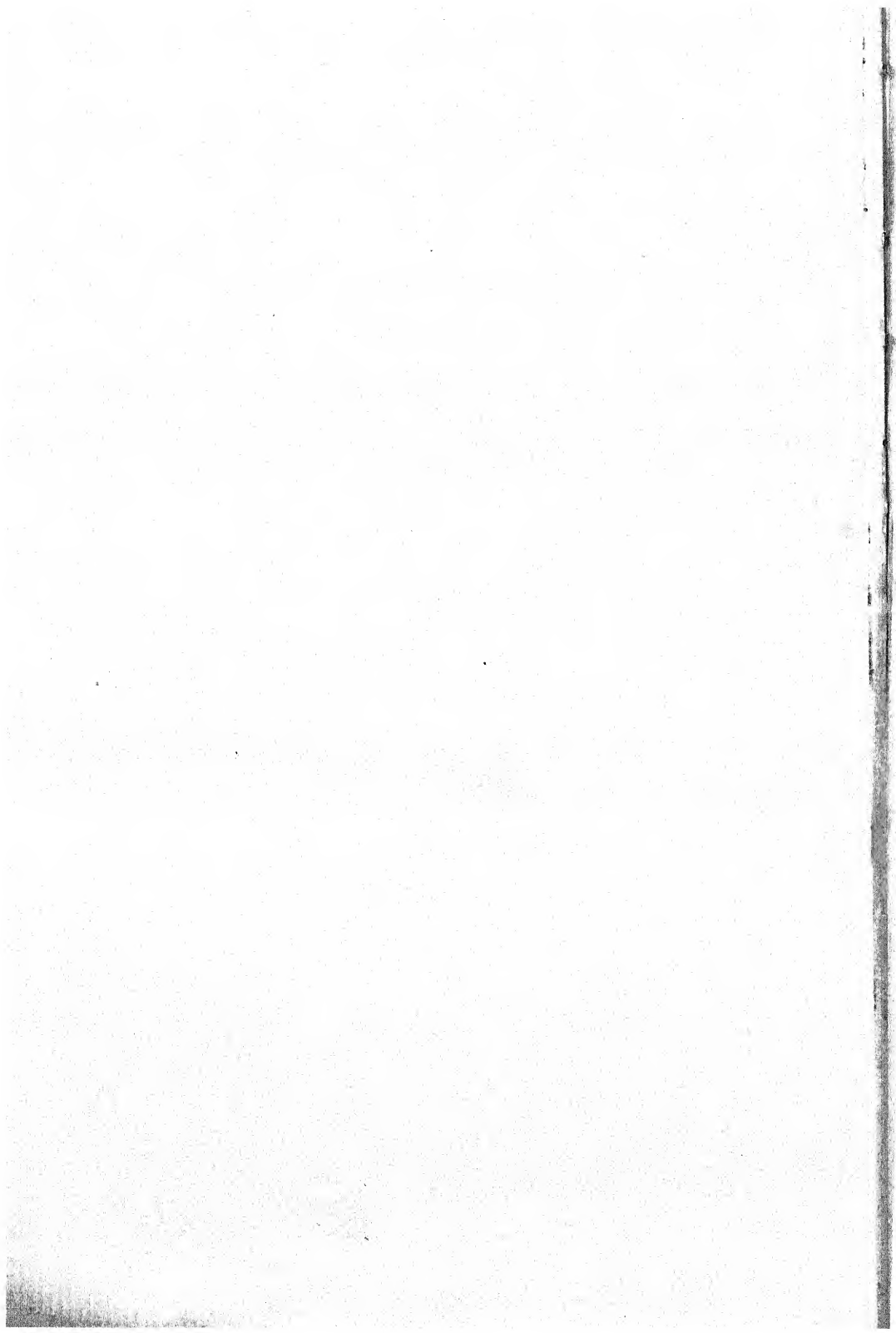
FIG. 335. Diagrammatic representation of the relationship of genes and chromosomes forming linkage groups. To the left at I, a pair of homologous chromosomes, each with a group of genes *A* and *a* to *G* and *g*. These genes constitute a linkage group. To the right at II, a second pair of homologous chromosomes of different shape with genes *M* and *m* to *T* and *t* forming a second linkage group.

and animals, has expanded and extended the conception of heredity as proposed by Mendel in 1866. The fundamental idea of heredity, *viz.*, segregation, has remained substantially as Mendel proposed it. With the increased knowledge of the chromosomes and their behavior, certain new ideas of heredity have come to be held generally among students of genetics. It has been found that occasionally two characters or traits tend to be inherited together, not segregating as normally expected. When characters tend to be inherited together, they are said to be linked and the condition is called **linkage**. The **physical, or material, basis of linkage** is to be sought in the relation of the genes to the chromosomes, as described in the following paragraph.

Since the number of chromosomes in any species of organism is quite definitely limited, and the characters or traits of complex organisms are

very numerous—from a practical working basis almost unlimited—it follows that there are a great many more genes conditioning these numerous traits than there are chromosomes. Naturally then there are many genes associated with each chromosome. It has been found, for all organisms thoroughly studied, that each chromosome carries a definite group of genes (Fig. 335). Two or more genes carried on a certain chromosome are said to be linked. All the genes on a pair of homologous chromosomes collectively form a linkage group. In general, the genes on a chromosome are inherited exactly as a single gene. This is true because the behavior of a single gene, or of a group of linked genes, follows the behavior of the chromosome which carries either a single gene or a group of genes. When reference is made to the inheritance and behavior of a single gene on a certain chromosome, it should be kept in mind that actually there is a whole group of genes on the chromosome but that only a single gene is being considered at that time. Two or more genes considered at one time are linked if they are both located on the same chromosome.

Linkage of genes also leads to numerical modifications of the dihybrid ratios. *These modifications constitute an exception to Mendel's second law of heredity, the assortment of genes.* This exception is based upon (1) the relationship of the linked genes to the chromosomes and (2) the behavior of chromosomes during meiosis, which influences the segregation of genes.



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